

ABSTRACT

Title of dissertation: THE EFFECT OF MENTAL STRESS ON BRAIN DYNAMICS AND PERFORMANCE RELATED TO ATTENTION CONTROL DURING A VIGILANCE TASK: AN ELECTROENCEPHALOGRAPHIC INVESTIGATION

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2013

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Anxiety can increase distractibility and undermine the quality of psychomotor performance. Models of attention processing postulate that anxiety consumes limited executive resources necessary for maintaining goal-oriented, “top-down” attention control and suppressing stimulus-driven “bottom-up” distraction. Attention Control Theory (ACT) predicts that anxiety adversely affects the efficiency, and particularly inhibitory components of executive, frontally mediated top-down attention control. We used two approaches for examining this model. First, though attention affects synchrony among neural structures, information regarding how human oscillatory patterns (measured with electroencephalography, EEG) change as state anxiety increases is limited. Second, while anxiety affects the balance between top-down and bottom-up mechanisms, to our knowledge no one has yet measured anxiety’s effect on attention using a neural measure of top-down control in conjunction with more traditional bottom-up measures of attention capture (e.g., the P3 event related

potential, or ERP). **Purpose:** Study 1 examines the oscillatory patterns (spectral dynamics) of the cortex in order to investigate whether frontal regions exhibit patterns of reduced efficiency and altered networking with posterior regions during threat of shock. In order to assess the relationship between top-down and bottom-up attention dynamics, Study 2 uses the same threat protocol to measure attention-directed top-down modulation of sensory signaling (steady-state visual evoked potential, or ssVEP modulation) and of bottom-up attention capture by discrete targets and distractors (Event Related Potentials, ERPs). **Results:** The spectral analyses in Study 1 suggest decreased processing efficiency and decreased frontal networking (coherence) with more posterior regions as anxiety increased. Reduced coherence, however, could indicate either increased or decreased top-down focus; Study 2 provides more insight. Neural responses to task-relevant targets (ERPs) diminished as threat increased, while responses to task-irrelevant distractors remained unchanged. Contrary to what ACT would predict, we observed an increase in attention modulation of an ssVEP frequency associated with amplifying the task-relevant signal and no change in an ssVEP associated with inhibiting task-irrelevant stimuli. These findings suggest top-down attention control increased under threat, but was not enough to prevent degraded processing of task-relevant targets coincident with reduced efficiency on task performance. Implications and suggestions for refining ACT are discussed.

**The effect of mental stress on brain dynamics and performance related to
attention control during a vigilance task:
An electroencephalographic investigation**
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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2013

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Acknowledgements. I would like to acknowledge and thank the following people for their contributions to this work. Claire Stevens, Matt Ballew, Kyle Jaquess, and Li-Chuan Lo for assistance in data collection; Alessandro Prosacco, Hyuck Oh, and Peter Agada for technical assistance; Dr. Christian Grillon and Dr. Bethany Reeb-Sutherland for protocol guidance; Dr. Greg Hancock for statistical guidance, Dr. Petra Bradley for extensive help with theoretical, statistical and draft revision; each of my committee members (Dr. Joseph Dien, Dr. Charles A. Morgan, III, Dr. Elizabeth Quinlan, Dr. Stephen Roth and Dr. Carson Smith) for their individual contributions to the research design, analytic help and general mentorship; Dr. Bradley D. Hatfield, my advisor, who guided me at every step in my doctoral education; and Adam Russell, my dear husband, for his unyielding support.

I would like to dedicate this dissertation to my mother, Dr. Bernadine Healy. She showed the world how much science could gain from women; she showed me how much I could gain from science.

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Study 1

Inefficiency and reductions in frontal networking are associated with increases in state anxiety: an electroencephalographic (EEG) investigation of the interaction between anxiety and top-down attention control during a target-detection task.

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Abstract: Previous research has revealed that anxiety affects performance partly by shifting limited attention resources away from task-relevant goal-oriented processing in favor of stimulus-driven processing. Views differ as to whether anxiety erodes cognitive control, thereby reducing frontal activity, or if it causes an increase in frontal activity as adaptive performers compensate for eroded executive control. Though attention affects synchrony among neural structures, to date there is little evidence of how oscillatory patterns as measured by electroencephalographic (EEG) change as a result of increased state anxiety.

Purpose: The present study examines the cortical dynamics and common oscillatory patterns between frontal and more posterior regions of the brain in order to investigate whether anxiety reduces processing efficiency, and if frontal structures exhibit increased activity as state anxiety increases. **Methods.** Electroencephalography (EEG) was recorded from 50 participants during an attention-demanding target detection task under three levels of threat recorded over two days. During the Shock Day (SD) finger electrodes were attached during both Safe and Threat conditions, but participants were only at acute risk of

shock during the Threat trials. Finger electrodes were not attached during the No Shock Day (NSD). If performers recruit additional resources to maintain performance under increased threat, the cortex should show increases in activity (beta and gamma power) and a decrease in frontal connectivity (coherence) with more posterior brain regions. Likewise, if anxiety compromises volitional 'top-down' attention control, frontal networking with sensory processing regions should likewise decrease. **Results:** Processing and performance became less efficient under the highest level of threat as high-alpha power desynchronized and reaction times slowed. A decrease in frontal coherence suggests a decoupling between frontal and more posterior regions and an increase in temporal beta and gamma power suggested this decoupling may be due to increased localized processing irrespective of top-down control. These findings support theories that increased anxiety erodes processing efficiency, but did not find that increased effort to compensate for this inefficiency was frontally mediated.

1.0 Introduction

Stress and anxiety shift the balance between top-down goal-oriented attention processing and bottom-up stimulus-driven attention mechanisms (see Arnsten, 2009 and Robinson, Vytal, Cornwell, & Grillon, 2013 for reviews in animals and humans, respectively). While it is well accepted that anxiety increases early sensory processing (Robinson, Letkiewicz, Overstreet, Ernst, & Grillon, 2011; Shackman, Maxwell, McMenemy, Greischar, & Davidson, 2011), how anxiety affects top-down control and processing of incoming sensory stimuli is less well understood. Central executive function (Baddeley, 1996) and its anatomical correlates direct top-down attention control, which selectively amplifies task-relevant signals, and inhibits task-irrelevant information from incoming sensory processing streams (Corbetta & Shulman, 2002). Primate (Arnsten, 2009) and human studies (Demeter, Hernandez-Garcia, Sarter, & Lustig, 2011) suggest a set of regions in the frontal cortex bias sensory signaling earlier in the processing hierarchy, and may do so by synchronizing signals for stimuli of interest and disrupting synchrony of neurons tuned to irrelevant stimuli (Engel, Fries, & Singer, 2001). Current theories have different views on whether anxiety impairs prefrontal function, thereby reducing the activity of these structures (Bishop, Jenkins, & Lawrence, 2006; Bishop, Duncan, Brett, & Lawrence, 2004) or reduces the efficiency of top-down function increasing prefrontal control in an effort to compensate (Eysenck & Derakshan, 2011; Eysenck, Derakshan, Santos, & Calvo, 2007). Though a great deal of behavioral, fMRI and event-related-potential (ERP) studies have examined how anxiogenic contexts and

stimuli affect attention systems, and though it is known that attention affects the oscillatory patterns within and among these regions, it is not clear how anxiety affects human cortical oscillatory patterns and dynamics associated with attention.

Attention Control Theory. Attention Control Theory (ACT, (Eysenck et al., 2007) evolved from Processing Efficiency Theory (PET, Eysenck & Calvo, 1992) which postulates anxiety impairs performance efficiency – or a decreased ratio of effectiveness to effort – even if it does not always affect performance. Likewise, ACT's primary hypothesis is that anxiety will impair the efficiency of attention control, which is to say additional neural resources are necessary to maintain performance. The majority of the evidence for this view has come from behavioral evidence including patterns of time/accuracy tradeoffs, increases in effort to complete cognitive tasks, and the costs associated with high-conflict tasks (Ansari & Derakshan, 2011; Righi, Mecacci, & Viggiano, 2009; Savostyanov et al., 2009). Observations that psychomotor neural efficiency is a hallmark of superior performance (Deeny, Hillman, Janelle, & Hatfield, 2003); that visual search and gaze behavior becomes inefficient when performers are anxious (Janelle, 2002) and tradeoffs between speed and accuracy on reaction time tasks during threat of shock (Hu, Bauer, Padmala, & Pessoa, 2012) further support this element of ACT.

Other well-replicated findings in neural imaging studies have shown patterns that are difficult to reconcile in terms of ACT. In particular, functional Magnetic Resonance Imaging (fMRI) studies show a negative correlation between state anxiety and activation among frontal regions specifically implicated in top-down attention control (i.e., dlPFC and vlPFC; Bishop, 2007; 2008a; Bishop et al., 2006). Trait anxious individuals also show a decrease in frontal activation compared to lower-anxious individuals (Bishop, 2008b). Interestingly, these effects are blocked (Bishop, 2007) and even reversed (Bishop, 2008b) in high load conditions compared to low-load conditions. ACT's efficiency hypothesis would predict the reverse; if anxiety and efficiency are inversely related, it would become more difficult to maintain performance as anxiety increased. While there are other structures involved in directing top-down attention along the dorsal attention network (DAN, Fox et al., 2005), such as the frontal eye fields (FEF) and intra-parietal junction (IPJ) not investigated in neuroimaging literature that may follow different patterns of activation and lend support to ACT, currently ACT does not provide a means to explain anxiety-induced decreases in frontal activation.

Animal research of neurochemical systems provides insight into mechanisms that might underlie these phenomena. The interaction of anxiety of top-down attention selection has been linked to the function of noradrenaline and dopamine receptors in the prefrontal cortex. Both dopamine and noradrenaline are necessary for enhancing selective attention by amplifying firing to preferred

stimuli (task-relevant) and suppressing neural firing to non-preferred (distracting) stimuli. Indeed, dopamine is linked to coupling of attention networks (Dang, O'Neil, & Jagust, 2012). Stress increases the presence of both chemicals and too much of either will over-suppress prefrontal firing, diminishing responses to all stimuli in a non-discriminative manner, thus eliminating top-down selectivity. While the patterns in catecholamine-related suppression would not support a model of increased frontal activity as anxiety increases, increased *effort* has been linked to top-down stimulation of additional acetylcholine release from the basal forebrain (Sarter, Gehring, & Kozak, 2006), which would subsequently increase cortical activity.

The debate remains active, and the data apparently contradictory. While fMRI's spatial resolution is convincing, the Blood Oxygen Level Dependent (BOLD) signal is a measure of metabolism used as a proxy for neural activity. This means an inhibitory circuit may be more metabolically active, but could be actively *inhibiting* function (e.g., GABAergic inhibition). Measures of synchronous and asynchronous activity within and between regions are more direct indicators of neural function. Primate and cat studies have demonstrated attention synchronizes oscillatory signals among neurons that fire in response to stimuli of interest, and disrupts synchronous firing among neurons sensitive to to-be-ignored stimuli. Such synchrony occurs not just within a given region, such as V4 for instance, but also between regions, such as between occipital, parietal and motor cortex during visual-motor task performance (Roelfsema, Engel, König, &

Singer, 1997). While it is still up for debate as to whether this sort of synchronization among neural populations is what 'binds' sensory representations up and down the processing hierarchy (Engel & Singer, 2001; Singer & Gray, 1995), these studies nonetheless link oscillatory patterns to top-down attention control.

Thus, a study examining the spectral content and patterns of oscillatory activity under various levels of state anxiety during an attention task, though not as spatially precise as fMRI, would provide a direct measure of neural activity and might offer additional insight into how anxiety affects attention control mechanisms. While there has been extensive work examining the relationship between state anxiety and attention control mechanisms (under threat of shock and in response to threatening stimuli) to our knowledge the regional spectral dynamics, and regional networking of attention control in a threat-of-shock paradigm has not yet been explored.

Spectral analysis of electroencephalographic (EEG) recordings provides an index of relative synchronous cortical activity among neural populations; an increase in power within a frequency band of interest (for instance, alpha band consists of frequencies between 8-13Hz) reflects more synchronous oscillatory activity among neural populations within that range. Different frequency bands have been associated with distinct cognitive processes. For instance, and of interest for the present study, frontal theta power (4-7 Hz) is directly related to goal-

oriented sustained attention (Mizuki, Takii, Tanaka, Tanaka, & Inanaga, 1982; Sauseng, Hoppe, Klimesch, Gerloff, & Hummel, 2007). Likewise, alpha power is inversely related to externally-oriented engagement. A relative decrease in low-alpha power (8-10Hz) may be indicative of an increase in generalized arousal, whereas a decrease in high-alpha power (10-12 Hz) reflects greater task-related effort (Klimesch, Schimke, & Pfurtscheller, 1993) and attentional demands (Ray & Cole, 1985). Beta (13-30 Hz) has been linked to cognitive as well as emotional processing (Ray & Cole, 1985) and increases in gamma (30-70 Hz) occur during attention tasks (Gruber, Müller, Keil, & Elbert, 1999; Müller, Gruber, & Keil, 2000; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998)

If anxiety compromises top-down frontally-directed attention engagement, we should observe a decrease in frontal theta power as threat increases. Likewise, if ACT's prediction that frontal activity will increase with anxiety is correct, we would expect to see a decrease in high-alpha power in frontal regions reflecting an increase in task-oriented activity. More specifically, changes in high-alpha power in response to threat should reflect perturbation in attention-directed task-specific processing, while low-alpha power (8-10Hz) should decrease in response to a generalized increase in arousal in response to threat.

Because attention control is inherently a multi-regional function, understanding the relationship between attention and anxiety requires investigation of inter-regional activity as much as intra-regional activity. Coherence between electrode

sites is a statistical representation of the correlation (Pearson's R) of spectral content recorded at those sites; increased coherence between electrodes suggests increased communication between the regions underlying those electrodes (Nunez, 1995; Fries, 2005). According to Engel, et al., "large-scale coherence could be one of the correlates for top-down control" (Engel et al., 2001).

Thus, coherence should reflect anxiety-induced shifts away from top-down attention control mechanisms. When participants – guided by a therapist – were asked to imagine and engage in an anxious state, there was an observable decrease in coherence between frontal and central regions (Hinrichs & Machleidt, 1992), which may reflect a reduction in frontal executive control. Likewise, lower coherence between frontal and posterior sites among trait anxious individuals is associated with 'looser' frontal emotional control and regulation of posterior regions (Reiser et al., 2012). However, in normal circumstances healthy populations typically regulate emotional responses to threatening stimuli and in such cases there are increases in coherence between frontal and more posterior regions. For instance, coherence between frontal and tempo-parietal regions increased in response to threatening images (Miskovic & Schmidt, 2010) and film clips (Schellberg, Besthorn, Klos, & Gasser, 1990) indicating greater frontal control of posterior regions in response to emotionally loaded stimuli. In another sample coherence increased in low anxious participants and decreased in high anxious individuals in response to threatening

images (Aftanas, Lotova, Koshkarov, & Popov, 1998) suggesting an increase in coherence may reflect an adaptive response to threat.

Threatening stimuli present a rather mild emotional challenge however, and the abovementioned studies did not examine cortical dynamics during sustained attention. If increased state anxiety shifts attention bias towards processing environmental stimuli and away from goal-oriented executive-driven processing, we should observe a drop in frontal coherence with other regions suggesting a decrease in frontal

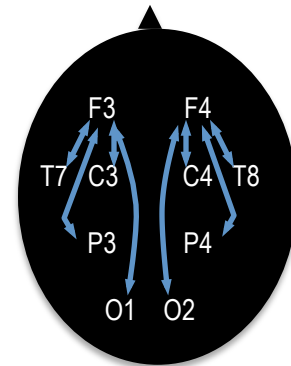


Figure 1. Coherence analysis between frontal and more posterior electrode sites. Lines represent pairs of electrodes tested.

communication with stimulus processing areas (central, temporal and parietal, see Figure 1). In particular, we will examine low-alpha (8-10 Hz), high-alpha (11-13Hz) and beta (13-30 Hz) coherence for two reasons: first, these frequency bands are most reflective of global communication whereas higher frequency bands (i.e. gamma) reflect intraregional cortico-cortical communication (Nunez, 1995); and, second the greater the distance between electrodes the more likely high frequency bands will exhibit high, but unrelated coherences (i.e., elevated risk of Type I error) (Srinivasan, Winter, Ding, & Nunez, 2007) .

To examine the cortical dynamics of sustained attention under various states of anxiety, we analyzed the spectral content of electroencephalographic (EEG) data

collected from a previous sample of 50 individuals over the course of two testing days, and three levels of threat. If anxiety erodes attentional efficiency and requires greater effort to maintain performance we should observe relative reduction in high-alpha in frontal sites, and increased coherence between frontal and more posterior regions.

2. Methods

We analyzed the spectral content from a previously collected sample (N = 50, f = 25) healthy, right-handed, college-age participants who performed a simple target detection task under three levels of stress over two sessions. The sample was screened for medication or symptoms of depression, anxiety disorders, and attention deficit disorders.

Anxiety Manipulation. Data were collected over the course of two testing sessions, a “Shock Day” (SD) and a “No-Shock Day” (NSD). These days were counterbalanced for order and held at the same time of day for each participant, at least a day but no longer than two weeks apart. During the SD participants wore electrodes on their third (“ring”) and fourth (“pinky”) left fingers that delivered a mild 4mA, 100ms electric shock (Colbourn Instruments). The SD consisted of “Safe” and “Threat” trials. Participants were at risk of receiving a shock at any point during the Threat trials, and were at no risk of receiving a shock during the Safe trials. Shock delivery was not linked to task performance and occurred at the same time during the course of the SD for all participants. During the NSD session participants did not wear the electrodes and all trials

presented were Safe trials. Because the participants were not wearing electrodes during the NSD, the Safe trials on the NSD were less threatening than the Safe trials on the SD; for the purposes of clarity we refer to these as “NSD” trials. The resulting three conditions were, in order of increasing threat: No Shock Day (NSD) < Safe < Threat. Differences between the NSD and SD trials should reflect contextual fear and generalized arousal, whereas differences between the Safe and Threat trials on the SD reflect more specific cued threat responses.

Target Detection Task. Participants were asked to hit a button as quickly and accurately as possible after detecting a digit among one of two alphanumeric sequences, which appeared 9 cm laterally from the center of 19” Dell monitor, without shifting their gaze away from a center fixation cross. A screen preceded each trial instructing the participant attend to either the left or right sequence, and whether the trial was a Safe or Threat condition. On each day there were four blocks of 25 trials each, separated by 1-2 minutes of rest. The Shock Day (SD) consisted of mixed-trial blocks and the NSD consisted of only Safe trials. Each trial lasted 10 seconds with 3 seconds rest between trials. The experiment was written in, and controlled by Presentation® software (Version 0.70, www.neurobs.com) on a desktop PC (Dell, Windows 2007 operating system).

EEG. Researchers recorded from thirty two active electrode channels arranged according to the 10-20 system (Jasper, 1958) at 1000Hz sampling frequency using the BrainVision atciCAP system (Brain Products, Munich, Germany). An

online reference to the left ear was later re-referenced offline to an average of both ears. Four additional electrodes were placed around the eye to detect electro-ocular movements and to quantify eyeblink startle responses.

Startle. Startle eyeblink magnitude is linked to amygdala activation and was used as a physiological index of state anxiety. The startle probes were white noise bursts (100ms, 60 dBA against ~48 dBA ambient noise) presented randomly throughout the testing session. Startle data were processed and quantified in accordance with the standards outlined in Blumenthal (Blumenthal et al., 2005). Data from the active startle electrode (lower-eyelid, below the pupil) were re-referenced against the outer startle electrode (lower eyelid, below the corner of the eye). Signals were band-pass filtered (28-40Hz with a 4th order Butterworth), rectified, smoothed (FIR Kaiser), visually inspected for non-startle artifact and averaged. Standardized area under the curve was calculated for each participant's data from 50ms-120ms after noiseburst onset for each condition.

Signal Processing and Data Reduction. All off-line filtering was performed in MATLAB. Shock and startle trials were removed from analysis and to maintain equal signal-to-noise ratio, a random selection of half of the Safe trials on the NSD were discarded so that we analyzed an equal number of NSD, Safe and Threat trials. Each 10-second trial was inspected for visual artifact and averaged across conditions.

Spectral Power. A fourth order Butterworth (0.1-100 Hz) with a 60 Hz notch filter was applied to each of the resulting time series. Resulting values were averaged across frequency bands.

Coherence. We computed coherence values in MATLAB (The MathWorks, Inc. 2010) between electrode pairs of interest (F3-C3, F4-C4, F3-P3, F4-P4, F3-T7, F4-T8, F3-O1, F4-O2). Resulting values were averaged across the low-alpha (8-10Hz), high-alpha (11-13 Hz) and beta (13-30 Hz) frequency bands.

Statistical approach. Startle and performance data were entered into a one-way, repeated measures ANOVA with three levels for condition. Subsequent pairwise comparisons were Bonferroni corrected. Spectral power data were entered into a 3 (condition: NSD, Safe, Threat) x 2 (hemisphere: left, right) x 5 (region: frontal, central, parietal, temporal, occipital) repeated measures ANOVA. Frontal coherence values were entered into a 3 (condition) x 2 (hemisphere) x 4 (regional pair: F-C, F-P, F-T, F-O) repeated measures ANOVA. The degrees of freedom for any results that violated the sphericity assumption of the linear model were Greenhouse-Geisser corrected; all p values reported reflect corrections when necessary, and post hoc comparisons corrected using Tukey's HSD method.

3.0 Results

3.1 Behavior, and physiological response to threat.

Startle. Startle was significantly potentiated as threat increased across condition ($F_{(2, 48)} = 48.28, p < .001$). Startle_{Safe} was significantly greater than Startle_{NSD} indicating there was a general amygdala activation associated with the Safe trials (contextual threat) compared to the NSD trials (Startle_{Safe} - Startle_{NSD} = 0.069, $p = .029$). Startle_{Threat} was also significantly greater than both Startle_{NSD} (Startle_{Threat} - Startle_{NSD} = 0.467, $p < .001$) and Startle_{Safe} (Startle_{Threat} - Startle_{Safe} = 0.408, $p < .001$). The magnitude of difference between Startle_{Safe} and Startle_{Threat} indicated a robust amygdala activation beyond that induced during the Safe conditions associated with the cued

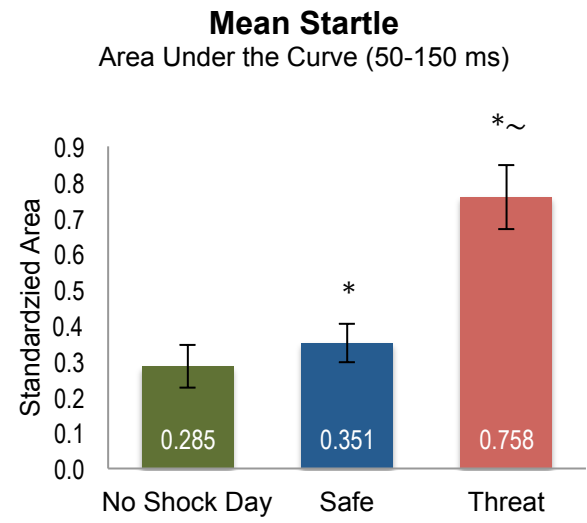
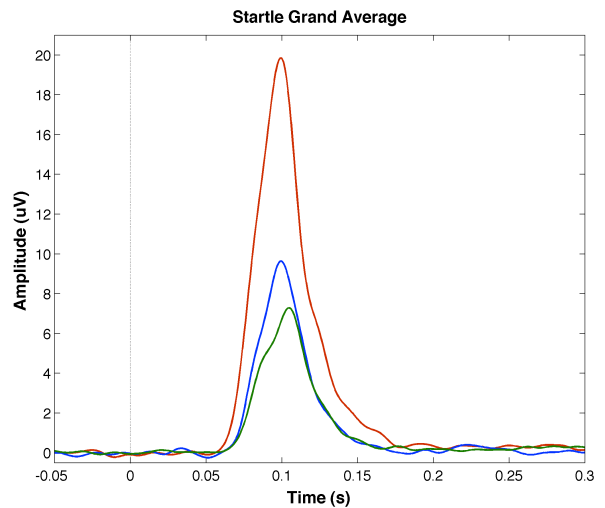


Figure 2. Startle was potentiated during both Safe and Threat conditions. Top panel: startle response waveforms for each condition. Bottom panel: Standardized area under the curve between 50 and 150 ms after noiseburst onset for each condition. Green: No Shock Day; Blue: Safe; Red: Threat. * indicates significant difference compared to NSD and ~ indicates significant differences compared to Safe.

threat.

Performance. While there was no significant difference in accuracy between condition ($F_{(2,98)} = .279$ $p = .7089$, $\eta^2 = .006$), there was a significant effect over the three levels for reaction times ($F_{(2,98)} = 7.72$, $p = .003$, $\eta^2 = .138$). Corrected pairwise comparisons revealed the RT_{Threat} condition was significantly slower than both the RT_{Safe} ($RT_{\text{Threat}} - RT_{\text{Safe}} = .012$ s, $p < .001$) and RT_{NSD} conditions ($RT_{\text{Threat}} - RT_{\text{NSD}} = .012$ s, $p = .012$).

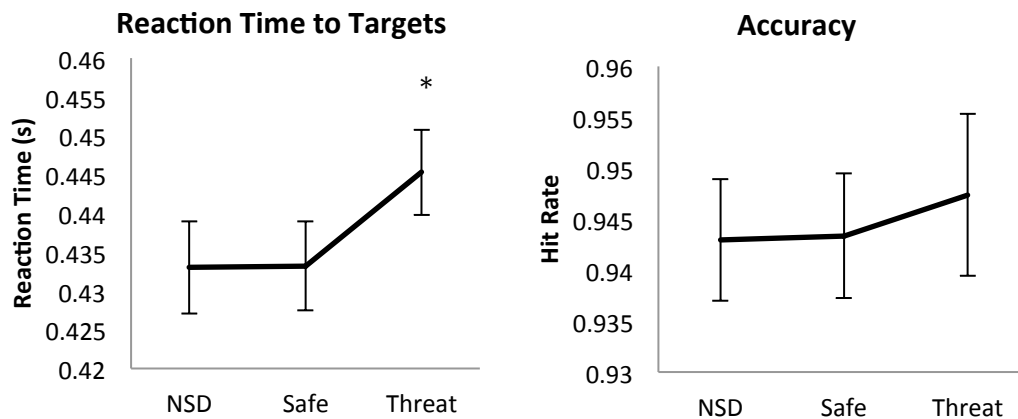


Figure 3. Performance for each condition. * indicates significant difference compared to NSD.

3.2. Spectral Analysis

Theta(4-7Hz). Statistical analysis indicated a condition x region interaction ($F_{(8,392)} = 4.043$, $p = .004$, $\eta^2 = .76$) and as expected, there was a decrease in frontal theta power between the conditions on the SD (Safe and Threat) and the NSD day. (Figure 4).

Low-alpha (8-10Hz). Statistical analysis for low-alpha power showed no significant main effects or interactions.

High-alpha(11-13Hz). Statistical analysis indicated a significant condition x hemisphere x region interaction in high-alpha power ($F_{(8,392)} = 3.057$, $p = .033$, $\eta^2 = .059$) such that power decreased as threat increased but to a greater degree in the right central region than in other areas. Collapsing across hemispheres, there was also a significant condition x region interaction ($F_{(3,392)} = 3.073$, $p = .028$, $\eta^2 = .059$) indicating high alpha decreased mainly in the central and parietal regions, but subsequent pair-wise comparisons did not survive correction. The main effect ($F_{(1,49)} =$, $p < .001$, $\eta^2 = .253$.) showed a significant desynchrony in high-alpha during the Threat condition compared to both the NSD and Safe

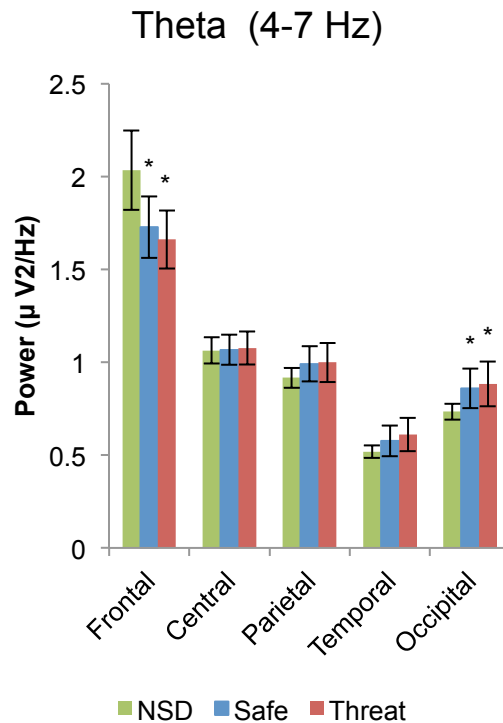


Figure 4. Theta power for the condition x region interaction. * indicates significance compared to NSD in the same region.

conditions (Figure 5). This indicates a general increase in task-related activity, mainly associated with the Threat condition and in the central and parietal regions.

High-alpha (10-13 Hz)

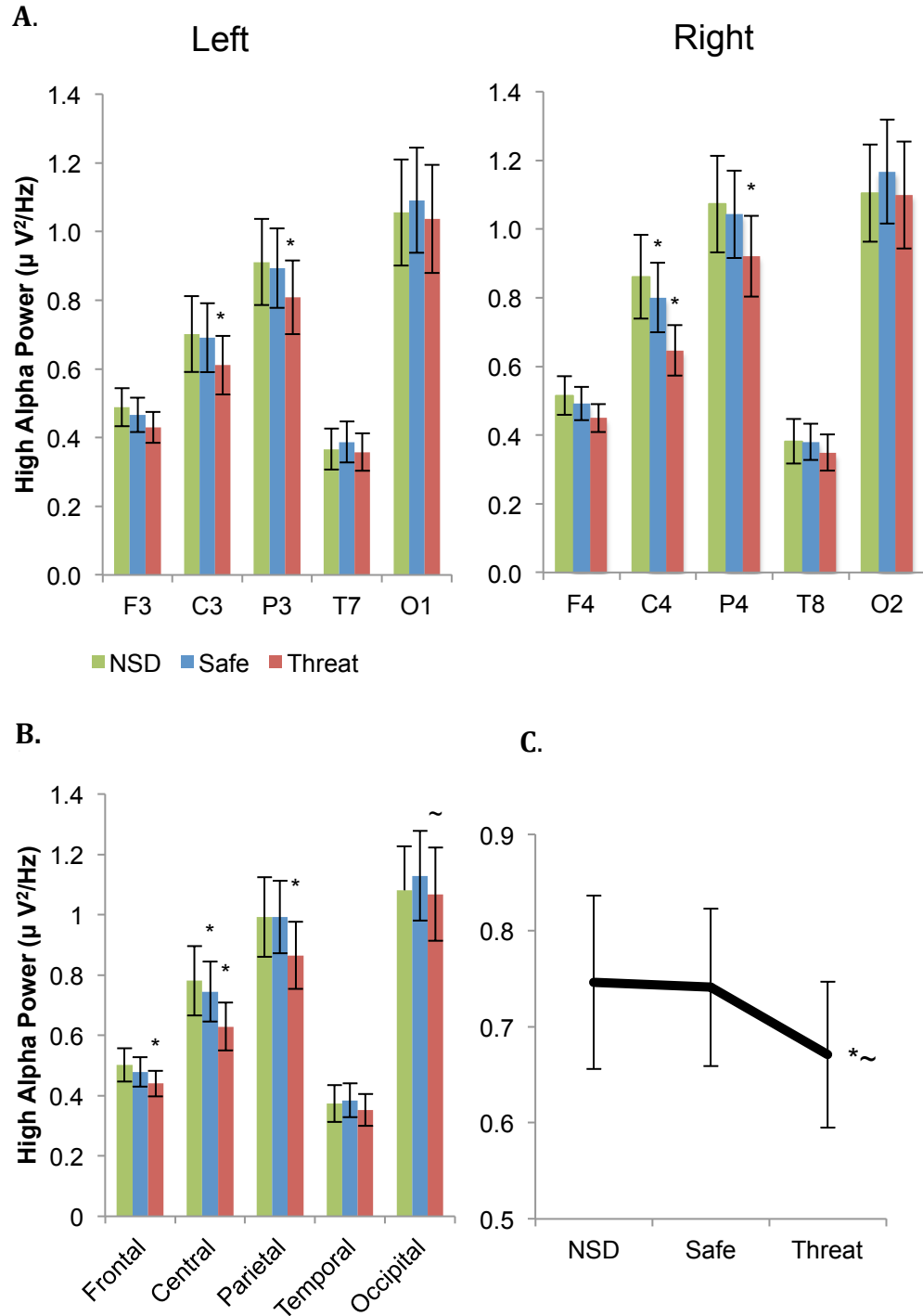


Figure 5: High-alpha Power (11-13Hz) **A.** Condition x hemisphere x region interaction. **B.** Condition x region interaction. **C.** Condition main effect. * indicates pairwise, corrected significance compared to the NSD condition in the same subgroup. ~ Indicates pairwise, corrected significance compared to the Safe condition in the same subgroup.

Beta(13-30 Hz). A condition x region interaction ($F_{(8,392)} = 5.349, p = .012, \eta^2 = .098$) indicated an increase in beta power in the temporal region between both conditions on the SD (Threat and Safe) and the NSD. A main effect for condition exhibited a similar pattern across the scalp ($F_{(2,98)} = 4.724, p = .002, \eta^2 = .088$) but pairwise comparisons did not survive post hoc analysis (Figure 6, A).

Gamma(30-70 Hz). A condition x region interaction ($F_{(8,392)} = 5.18, p = .004, \eta^2 = .096$) indicated an increase in gamma power between both conditions on the SD (Threat and Safe) and the NSD condition. The regional effect was large enough to drive a main effect for condition ($F_{(2,98)} = 8.425, p = .004, \eta^2 = .147$) (Figure 6, B and C).

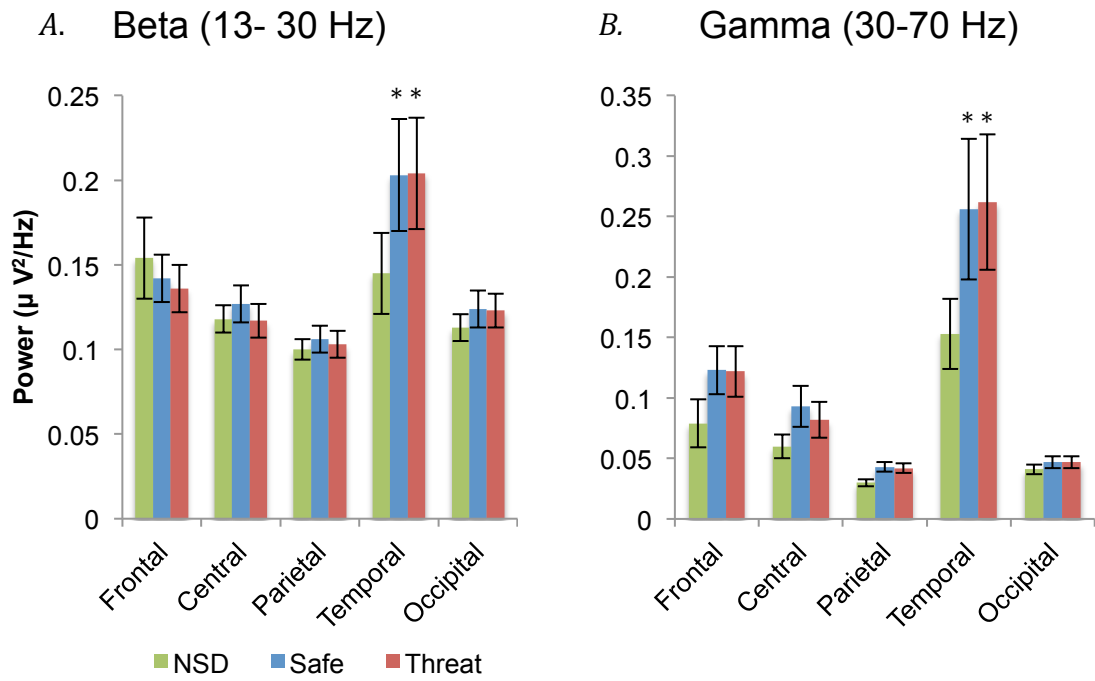
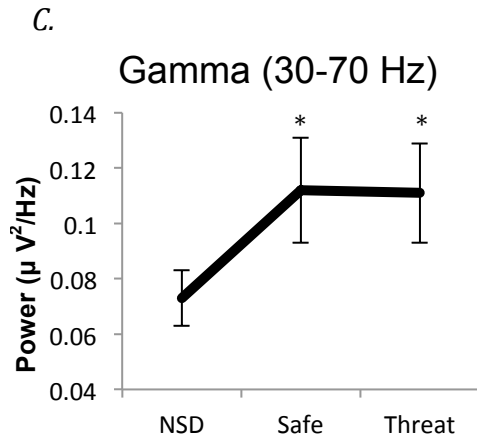


Figure 6. Threat-related increases in Beta and Gamma power. **A.** Condition X region interaction in beta power. **B.** Condition x region interaction in gamma power. **C.** Main effect for condition in gamma power. * indicates significant difference from NSD (in the same region for panels A and B).



3.3 Coherence

Low-alpha Coherence. Low-alpha coherence between frontal and more posterior regions revealed a significant condition x hemisphere x region interaction ($F_{(6, 294)} = 6.718, p < .001, \eta^2 = .121$) indicating greater coherence

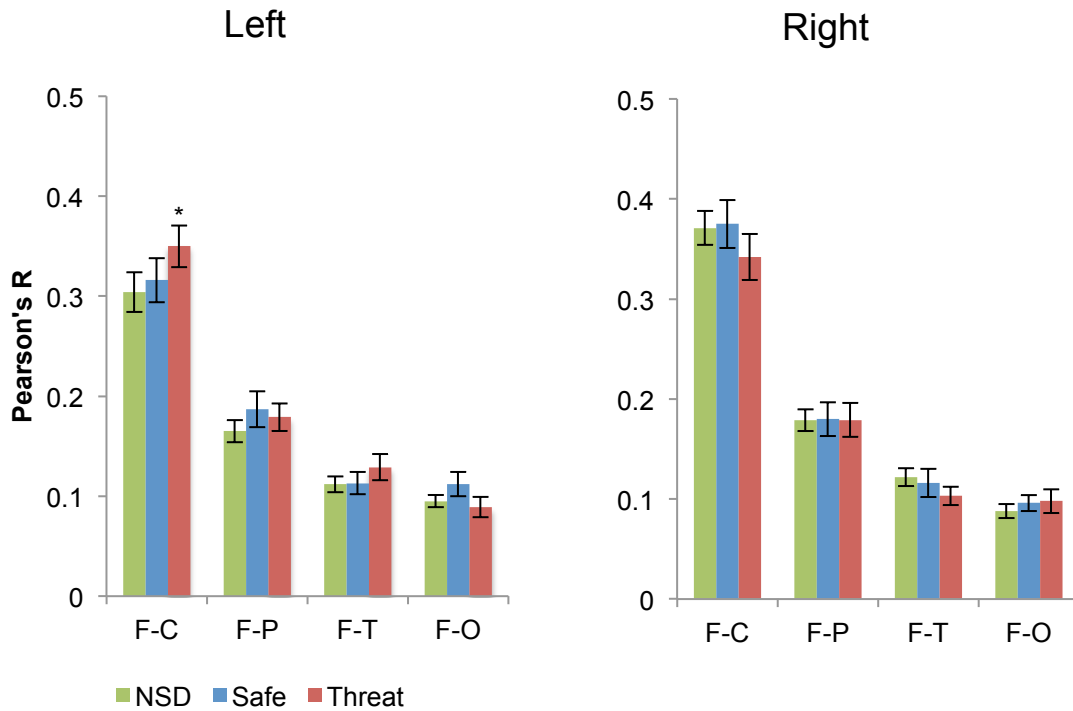


Figure 7. Low-alpha (8-10 Hz) coherence between frontal and posterior sites, condition x hemisphere x region interaction. * indicates pairwise corrected significance compared to NSD condition within the same subgroup.

between frontal and central electrodes during the threat condition compared to the NSD. Post hoc analysis revealed the left coherence between frontal and central regions during the Threat condition was significantly greater than coherence between the same electrodes during the NSD condition. The same was not true in the right hemisphere.

High-alpha Coherence. Frontal high-alpha coherence with more posterior regions was not sensitive to the experimental conditions.

Beta Coherence. Statistical analysis indicated a significant condition x hemisphere x region interaction ($F_{(6,294)} = 9.65, p < .001, \eta^2 = .164$). Collapsing across hemispheres, the condition x region interaction ($F_{(6,294)} = 39.88, p < .001, \eta^2 = .449$) was also significant, indicating frontal beta coherence with temporal and central regions dropped consistently regardless of hemisphere. Likewise, collapsed across regions, the condition x hemisphere interaction ($F_{(2,98)} = 5.93, p = .004, \eta^2 = .108$) was significant showing right hemisphere coherence with frontal regions dropped to a greater degree than left regions. Finally, there was a main effect for condition ($F_{(2,98)} = 34.618, p < .001, \eta^2 = .414$). Irrespective of hemisphere or region, overall beta coherence with frontal regions was lower during NSD conditions compared to both Shock Day conditions ($p < .001$, for both corrected pairwise comparisons). Beta coherence differences during Safe and Threat conditions on the Shock Day were not significantly different ($p = .063$).

Beta Coherence

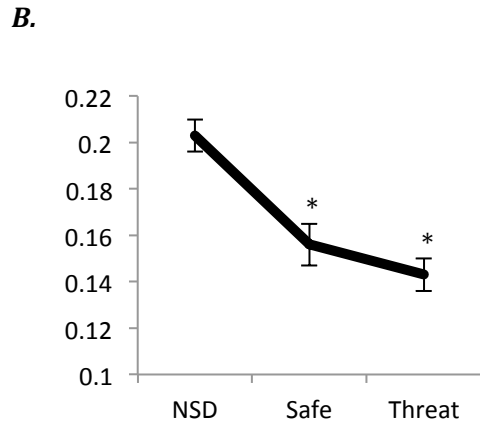
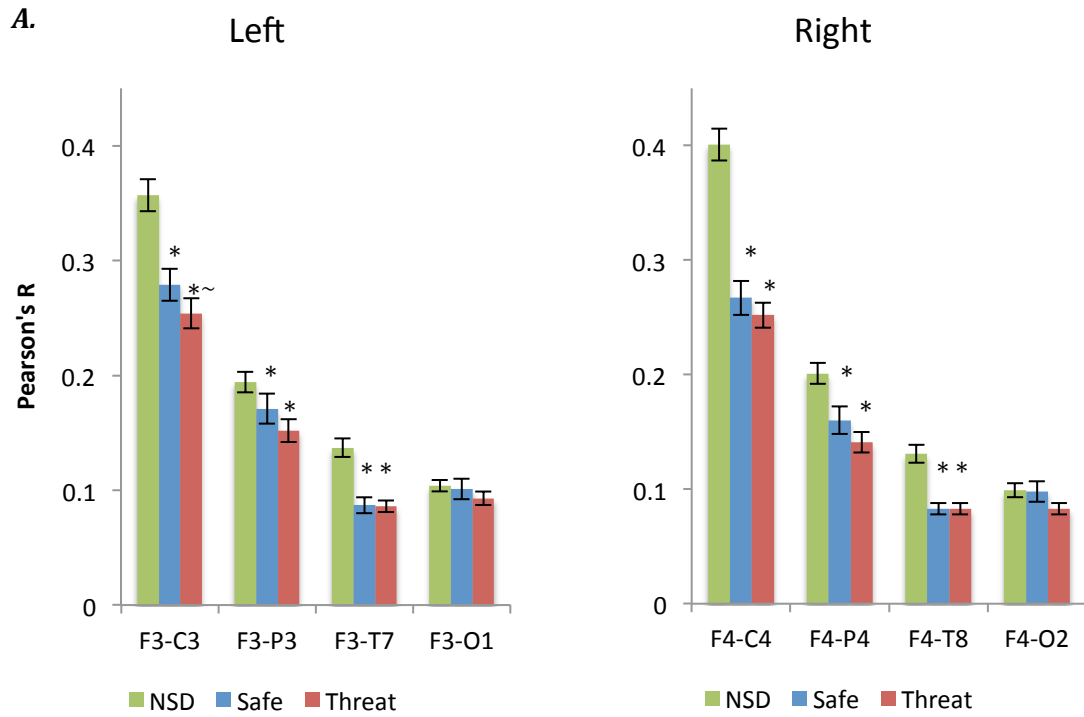


Figure 8: A. Beta coherence between frontal regions and more posterior scalp electrodes showed a significant drop in beta communication as threat increased in fronto-central, fronto-parietal and fronto-temporal regions. These effects were more pronounced in the right hemisphere between F4-C4 sites than on the left. **B.** The main effect for condition shows a significant drop in frontal beta coherence with more posterior regions in general. There were no significant effects between the Safe and Threat conditions on the SD.

4. Discussion

To investigate how anxiety affects top-down attention control the present study examined oscillatory cortical dynamics under three levels of threat while participants performed a sustained attention task. A decrease in frontal midline theta power and a broad reduction in beta coherence between frontal and more posterior regions suggest there may have been a relative shift away from top-down goal-directed processing. While there was a decrease in both performance and cortical efficiency to maintain accuracy on the task, this inefficiency was exhibited mainly in non-frontal regions, contrary to ACT's predictions. This may mean that reductions in efficiency in a healthy population are not the result of impaired executive function, but rather the result of a general increase in processing demand as a result of the imposed threat.

Startle potentiation confirmed the threat-of-shock protocol was successful in activating the amygdala. A small potentiation was associated with the Safe trials on the Shock Day compared to the No-Shock Day trials. Startle potentiation during Threat trials was more than six times greater than that of the Safe trial, indicating the amygdala was activated most when threat of shock was most acute.

The spectral analyses of these data provide evidence that increases in anxiety shift attention mechanisms away from top-down directed processing. Two pieces of evidence are relevant. First, volitional attention and

concentration during cognitive motor tasks are associated with increases in frontal midline theta power (Mizuki et al., 1982), but we observed a decrease in frontal theta power under both levels of anxiety (Safe and Threat conditions) compared to the No-shock Day (NSD). This pattern of reduced midline Theta power has also been observed in individuals viewing threatening stimuli (Aftanas, Pavlov, Reva, & Varlamov, 2003) while increases in frontal theta are associated with successful suppression in an anti-saccade task (Cornwell, Mueller, Kaplan, Grillon, & Ernst, 2012). Second, there was a drop in beta coherence between frontal and posterior regions (central, parietal and temporal) indicating a reduction in cortico-cortical communication between these regions. While the nature of the coherence correlation measure cannot determine directionality (even with phase analysis) the widespread reduction in coherence firing in the beta range suggests a general reduction in frontally-directed activity. The reduction in beta coherence between frontal and parietal regions is of particular note, since parietal beta power is positively related to cognitive tasks (Ray & Cole, 1985). A similar reduction in frontal coherence has been reported in high anxious individuals when watching aversive compared to neutral film clips (Aftanas et al., 1998), though the same was not true for low-anxious individuals. This pattern of reduced frontal coherence is opposite of that seen during other executive tasks, where working memory (Sarnthein, Petsche, Rappelsberger, Shaw, & Stein, 1998) and perceptual discrimination (Rodriguez et al., 1999) tasks were associated with generalized increases in coherence across regions. One could argue the coincident increase in beta power in temporal regions could

alone cause a relative drop in common communication (i.e., coherence) between frontal and temporal scalp sites, but this does not account for the relative drop in beta coherence between frontal and central, and frontal and parietal electrodes. In contrast to the broader decrease in frontal coherence in the beta frequency range, there was an isolated increase in low-alpha coherence between left-frontal and left-central electrode sites during the Threat compared to NSD trials. Low-alpha power is linked to thalamo-cortical projections that usually fluctuates with generalized arousal, meaning the effect might not be the result of cortico-cortical communication between left frontal and central regions, but rather that these regions are receiving common thalamic inputs. Overall, the dominant pattern is that of a generalized decrease in frontal coherence with other, more posterior regions.

There are notable limitations to our interpretation that the drop in beta coherence reflects a relative reduction in top-down attention control. First, it is possible that increased top-down *focus* would result in an overall decrease in common communication between frontal and more posterior regions. Attention is a function of both signal amplification and suppression. Direct local-field recordings in primates show attention synchronizes signals for features of interest, and actively desynchronizes those outside of focus (Engel et al., 2001). Thus, if anxiety narrows attention to focus only on task-relevant information and suppress (or desynchronize) all other task-irrelevant information (Easterbrook, 1959) then it is possible we would see an overall decrease in coherence despite an increase

in top-down selectivity. Second, while our interpretations are based on cortico-cortical models of top-down and bottom-up attention pathways (i.e., dorsal and ventral networks, respectively), a major component of top-down attention control involves a cholinergic circuit between prefrontal regions and the basal forebrain, especially during sustained attention tasks and in the face of increased distraction (Sarter, Givens, & Bruno, 2001). We can speculate that this may be the mechanism by which the brain is able to compensate for attention-related deficits or inefficiencies (Sarter et al., 2006)), but it may also offer a path for increased – albeit indirect – top-down control.

Anxiety-induced decreases in efficiency were not associated with frontal regions. The pattern of results provides partial support for ACT's model of anxiety and attention control. Slower reaction times were coincident with a drop in high-alpha power (indicative of increased activity) measured from central and parietal electrodes, but mainly during the most threatening condition (Threat trials). Accuracy on the target detection task did not change, thus participants maintained performance effectiveness but at an increased cost. Desynchrony in high-alpha power, an indicator of increased task-engagement, is likely linked to the drop in performance efficiency for two reasons. First, the drop in high-alpha power followed the same pattern as the alteration in performance; the only differences occurred during the greatest amount of anxiety (Threat trials). All other neural measures (theta, beta and gamma power, beta coherence), differed between both conditions on the Shock Day and the NSD. Second, high-alpha

desynchrony was located at central and parietal recording sites, which are closest to regions of sensorimotor integration such as that necessary to perform a target detection task. Together, this suggests that under the highest level of threat, a decrease in performance efficiency (slower RT) occurred at the same time as a decrease in cortical efficiency, which fits nicely with ACT's model.

The pattern of inefficiency across cortical regions, however, is not that predicted by ACT. The increase in beta and gamma power is an additional indicator of increased activity, as it is the opposite of that exhibited by efficient, expert performers compared to less-practiced individuals (Deeny et al., 2003; Haufler, Spalding, Santa Maria, & Hatfield, 2000). The effect, however, was isolated to temporal regions and no such increase in power in either band occurred in frontal or even central electrode sites, as ACT would predict (the small increase in gamma at frontal sites did not survive correction). The combined increase in beta power in temporal regions and a decrease in beta coherence with frontal regions suggests increased specialization in regional processing akin to that observed in novice marksmen compared to experts (Deeny, Haufler, Saffer, & Hatfield, 2009). While this further supports the notion of anxiety-induced inefficiency, it is not in the predicted frontal regions.

The sharp and localized rise in temporal beta power is notable and worthy of more consideration. The pattern is very similar to that seen when subjects were exposed to a painful cold pressor test (Chang, Arendt-Nielsen, & Chen, 2002). It

is unlikely, however, this common pattern was pain-related since participants in the present study only received four total shocks during the shock-day testing session, and most participants reported the shocks were aversive but not painful. Instead the common factor between the two studies may be threat, and the isolated location of the increased beta at temporal electrode sites could mean it is related to amygdala activation. Support for this possibility, however, is mixed. First, temporal beta power may be related to generalized emotional processing as a similar pattern was seen in response to both positive and negative emotional processing (Ray & Cole, 1985). Second, in the present study, the pattern of beta activity did not follow the pattern in startle potentiation, which is an index of amygdala activity. Startle potentiation showed the most marked difference between the Safe and Threat trials. Temporal beta power, on the other hand, was the same during Safe and Threat trials. The pattern is distinct and consistent with previous EEG studies including aversive contexts, but here again, there remain a number of possibilities for its origin.

It is worth noting that we did not observe evidence of a generalized increase in arousal. A substantial increase in state anxiety under threat would likely increase thalamic release of noradrenaline to the cerebral cortex, increasing cortical activation in a general manner. Low-alpha power reflects thalamo-cortical activity and is inversely related to increases in generalized arousal, thus the absence of a reduction in the low-alpha range suggests the threat manipulation, though aversive and enough to activate the amygdala, was not enough to induce

changes in arousal. We can speculate that this may reflect effective emotional regulation in a healthy population and it would be interesting to see if the pattern changed in a high- or clinically- anxious population.

Together these results suggest a decrease in processing efficiency as a result of increased anxiety, and a decrease in common communication between frontal and more-posterior cortical regions; it is unclear if the decrease in frontal-posterior communication is the result of an increase in focus at the exclusion of non-task-relevant stimuli, or the result of compromised top-down control. Because spectral analysis cannot provide concrete information about the directionality of the communication between electrode sites, future studies should look to incorporate concurrent measures of top-down and bottom-up processes to disentangle how anxiety affects each of the top-down and bottom up attention systems.

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Study 2

The dynamics of top-down attention control and bottom-up attention capture during threat of shock: An electroencephalographic investigation

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Abstract: Distractibility is a primary complaint among those who suffer from anxiety, which can affect the quality of psychomotor task performance and may be one reason why the majority of costs associated with anxiety-related disorders are attributed to lost workplace productivity. Models of attention processing are attributed to lost workplace productivity. Models of attention processing postulate that anxiety – whether situational or introduced by threatening stimuli – consumes limited executive resources that are necessary for maintaining goal-oriented, “top-down” attention control and suppressing stimulus-driven “bottom-up” distraction, particularly when perceptual load is low. Attention Control Theory (ACT) predicts that anxiety adversely affects the efficiency, and particularly inhibitory components of executive top-down attention control. While many studies have examined these phenomena, to the best of our knowledge none have measured anxiety’s effect on attention using a neural measure of top-down control in conjunction with more traditional bottom-up measures of attention capture (e.g., the P3 event related potential, or ERP). **Purpose:** In order to assess the relationship between top-down and bottom-up attention dynamics and anxiety, the present study measured attention-directed top-down modulation of sensory signaling (steady-state visual evoked potential, or ssVEP modulation) and of bottom-up attention capture by discrete targets and distractors (Event

Related Potentials, ERPs) under three levels of threat. **Results:** Behavioral, ssVEP and ERP findings show performance efficiency and neural responses to task-relevant targets were diminished as threat increased, while neural responses to salient task-irrelevant distractors remained unchanged. Though we expected anxiety would erode top-down control and would be inversely related to ssVEP modulation, we instead observed an increase in attention modulation of an ssVEP frequency associated with attention directed signal amplification and no change in the ssVEP frequency associated with inhibiting task-irrelevant stimuli. These findings suggest top-down attention control increased under threat, but was not enough to prevent degraded processing of task-relevant targets. Implications for current theories are discussed.

1. Introduction

Anxiety has long been known to affect human performance and although it has been the subject of countless studies, precisely how anxiety affects neural mechanisms underlying performance remains unclear. In some instances increased state anxiety can facilitate, while in other contexts it can degrade performance (for reviews see (Andersen, Hillyard, & Müller, 2008; Robinson, Vytal, Cornwell, & Grillon, 2013). Mechanisms of attention control underlie these differences as anxiety affects the balance between volitional ‘top-down’ goal-oriented stimulus processing and “bottom-up”, salience-driven processing as these two systems compete for limited cognitive resources. Generally, anxiety seems to increase sensitivity to bottom-up processing (Cornwell et al., 2007; Robinson, Letkiewicz, Overstreet, Ernst, & Grillon, 2011) and attention bias towards threatening stimuli (Koster, Crombez, Verschuere, Van Damme, & Wiersema, 2006; Lang, Bradley, & Cuthbert, 1998; Pessoa, 2009), but the exact way in which the two systems compete remains murky.

Attention is inherently limited, which is why researchers have traditionally characterized it as a “spotlight” (Easterbrook, 1959; Ekstrom, Roelfsema, Arsenault, Bonmassar, & Vanduffel, 2008; Gilbert & Li, 2013; Stein, Chiang, & König, 2000; Wachtel, 1967) that selectively highlights stimuli within a person’s attentional focus. Human behavioral and neuroimaging results (Andersen et al., 2008; Ekstrom et al., 2008; Engel, Fries, & Singer, 2001; Gilbert & Li, 2013;

Harris & Thiele, 2011; Stein et al., 2000; Treue, 2001) as well as direct neural recordings from mammals and non-human primates (for a review see (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Harris & Thiele, 2011)) have demonstrated that volitional attention selectively amplifies neural firing patterns as early in processing as that done in sensory cortex (Bridwell & Srinivasan, 2012; Treue, 2001) and the superior colliculus (Everling & Johnston, 2013). Engle et al. (2001) characterizes this executive-directed modulation of stimulus processing as “top-down” attention control in terms of anatomical processing hierarchies. Top-down attention also suppresses stimuli outside its focus (Arnsten, 2009; Bridwell & Srinivasan, 2012; Corbetta & Shulman, 2002; Gazzaley et al., 2005), putatively to prevent stimulus-driven “bottom-up” processes from ‘capturing’ limited resources and distracting them from a goal. Thus, volitional top-down attention control has two distinct mechanisms: amplifying task-relevant stimuli and suppressing stimuli that are task-irrelevant and potentially distracting.

Neuroanatomy and networks. Corbetta and Schulman (2002) identify distinct neuroanatomical regions and networks associated with top-down and bottom-up attention networks. Top-down networks include the dorsolateral prefrontal cortex (dlPFC) and anterior cingulate cortex (ACC), frontal eye fields (FEF), as well as regions associated with various forms of inhibition that include the dorsomedial PFC (DMPFC), right inferior PFC (rIPFC), left inferior frontal gyrus (lIFG) and ventromedial PFC (VMPFC) (Arnsten, 2009; Corbetta & Shulman, 2002; Gilbert

& Li, 2013; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). These regions are coordinated as part what is called the “Dorsal Attention Network” (Buschman & Miller, 2007; Corbetta & Shulman, 2002; Noudoost, Chang, Steinmetz, & Moore, 2010; Spreng et al., 2010) in which the Frontal Eye Fields coordinate with dorsal parietal regions to direct attention spatially towards goal-relevant stimuli.

Top-down control along this network amplifies the signals of preferred, incoming, task-relevant information at lower stages in visual processing hierarchies (Buschman & Miller, 2007; Gilbert & Li, 2013; Hubel & Wiesel, 1962; Noudoost et al., 2010). Direct field recordings in primates support this model as they have revealed that frontal regions fire before parietal structures during top-down processes (i.e., search tasks) indicating the frontal cortex ‘selects’ stimuli for preferential processing (Buschman & Miller, 2007; Corbetta & Shulman, 2002).

Bottom-up processing streams are driven by the intrinsic saliency of stimulus properties, such as color, shape, contrast and motion to which neurons in striate and extrastriate regions are ‘tuned’ (see Corbetta & Shulman, 2002 and Hubel & Wiesel, 1962, for example). In contrast to top-down processes, parietal structures fire prior to frontal regions in bottom-up tasks (aptly named “pop out” tasks, Buschman & Miller, 2007; Goodale & Milner, 1992) indicating that information from salient stimuli are relayed up processing hierarchies to capture attentional focus of frontal regions (Bishop, 2008a; Corbetta & Shulman, 2002;

Pessoa, 2008). This pattern of firing is opposite of that observed in the aforementioned top-down tasks, but also follows a different pathway. While top down signals are directed along dorsal streams to direct spatial attention, bottom up signals travel up a ventral processing stream (Bishop, 2007; Corbetta & Shulman, 2002) classically associated with identifying stimuli (coined by Goodale and Milner as the ventral “what” pathway; Goodale & Milner, 1992).

The balance between these two mechanisms enables adaptive filtering that directs attention towards potential environmental threats (stimulus-driven, bottom-up) and facilitates reflexive responses, but also allows us to focus attention on goal-oriented (executive-driven, top-down) tasks in the face of distraction. For these reasons the effect of anxiety on this balance of attention control has wide-reaching implications for everything from anxiety disorders and general workplace productivity to elite sport and military performance.

State Anxiety & Attention Control. Disentangling how anxiety affects these two separate and dynamic top-down and bottom-up mechanisms has been difficult. Most current theories of anxiety and attention control attempt to explain and incorporate myriad findings (see Bishop, 2007; 2008a; Eysenck & Derakshan, 2011; Eysenck, Derakshan, Santos, & Calvo, 2007 ; Pessoa, 2008; Robinson et al., 2013; Bishop, 2008a; Eysenck et al., 2007; Eysenck & Derakshan, 2011; Lang et al., 1998; and Robinson et al., 2011; 2013 for reviews and perspectives) but all agree generally that anxiety, whether introduced through threatening

stimuli (Bishop, 2008a; Robinson et al., 2013; Ansari & Derakshan, 2011; Lang et al., 1998) or threatening contexts (Pessoa, Padmala, Kenzer, & Bauer, 2012; Robinson et al., 2011; Robinson et al., 2011; 2013), shifts the balance from top-down goal-oriented processing towards bottom-up stimulus-driven processes (Figure 1). Under most circumstances, top-down control can suppress and “tune-out” task irrelevant stimuli allowing for efficient allocation of limited resources. In the face of threat, however, the bottom-up system can override that control, and capture attention to alert one to changing contexts or potential dangers.



Figure 1: The influence of anxiety on attentional mechanisms. Heightened anxiety increases the influence of bottom-up capture of limited attentional resources, increasing the influence of task-irrelevant stimuli (distractors).

Neurochemically, the interaction of anxiety of top-down attention selection has been linked to the function of noradrenaline and dopamine receptors in the prefrontal cortex. Both dopamine and noradrenaline are necessary for enhancing selective attention by amplifying firing to preferred (task-relevant) stimuli and suppressing neural firing to non-preferred (distracting) stimuli. Stress activates the amygdala which signals for release of both chemicals; while a small addition of catecholamine can improve selectivity and filtering, too much will over-suppress prefrontal firing, diminishing responses to all stimuli in a non-discriminative manner (review by Arnsten, 2009). This absence

of top-down prefrontal selectivity putatively increases reactivity to stimulus-driven bottom-up processing. Indeed, in humans anxious states increase sensitivity to stimulus-driven sensory changes (Cornwell et al., 2007). The behavioral outcome is that increased sensitivity facilitates reflexive, inflexible behavioral responses to environmental stimuli, and impairs flexible, executive-driven responses (Ansari & Derakshan, 2011; Eysenck et al., 2007; Eysenck & Derakshan, 2011; Friedman & Miyake, 2004; Pessoa et al., 2012; Robinson et al., 2011; Schupp et al., 2006). A remaining challenge, however, is that the PFC directs many cognitive processes, and while we know firing patterns are altered, it is still not clear how these chemical processes relate to specific cognitive elements of attention control.

Attention Control Theory (ACT) postulates that anxiety impairs the efficiency of executive control and, more specifically the inhibitory and task-switching components of executive function (Eysenck et al., 2007; Eysenck & Derakshan, 2011). Eroding inhibitory function – which normally prevent task-irrelevant stimuli from compromising performance (Friedman & Miyake, 2004) – allows salient, yet irrelevant stimuli to arbitrarily consume limited attention resources. Eysenck and Derakshan (2011) point primarily to evidence from anti-saccade tasks as evidence for compromised inhibition: there are costs on conflict trials, in which participants are instructed to look away from a cue, not seen in congruent trials during which participants look towards the cue. Anti-saccade tasks do not, however, distinguish between top-down control that inhibits a reflexive response

to a stimulus, and the top-down control necessary to inhibit potentially distracting stimuli from capturing attention in the first place. It thus remains unclear if anxiety impairs top-down suppression of signaling from task-irrelevant stimuli.

Measures of top-down and bottom-up attention. There is a notable lack of research that examines the neural dynamics of bottom-up and top-down attention *simultaneously* in anxiogenic compared to neutral conditions. Part of this lacuna is due to the practical difficulty associated with measuring endogenously generated top-down control in behaving humans. Bottom-up attentional-capture has long been quantified using a variety of Event Related Potential (ERP) paradigms (e.g., Dien, Spencer, & Donchin, 2004; Keil et al., 2007; Mittermeier et al., 2011; Robinson et al., 2013; Sawaki & Katayama, 2009; Schupp et al., 2006; 2004; Thierry & Roberts, 2007; Wachtel, 1967) in which investigators time-lock (to the millisecond) electroencephalographic measurements of neural activity to experimentally-presented stimuli. Greater amplitude or earlier latency of the waveform indicates more neural resources were deployed to, or facilitated processing of, the stimuli that elicited the ERP. Investigators cannot similarly time-lock EEG to endogenous top-down processes, in part because it is difficult to predict changes such as covert shifts and lapses in attention.

Combining bottom-up ERP measures with Steady State Visual Evoked Potentials (ssVEPs) (Müller & Hillyard, 2000) offers a possible solution. ssVEPs are continuous experimentally-induced neural frequency 'tags' that are sensitive to

endogenous top-down attentional focus, and easily measured with electroencephalography (EEG). A visual flicker presented at a specific frequency (say, 12Hz) will evoke that same frequency in visual processing regions of the cerebral cortex. Importantly, ssVEP amplitude is greatest when attention is devoted towards the driving flicker, and is suppressed when the flicker is unattended or actively ignored. While exogenous stimuli drive the ssVEP, when visual gaze is fixed the *modulation* of ssVEP amplitude is entirely endogenous and a function of top-down attentional control (Morgan, Hansen, & Hillyard, 1996). A greater difference between the amplitude of an ssVEP when the driving frequency is attended ($ssVEP_{Attend}$) and when ignored ($ssVEP_{Ignore}$) indicates more selective top-down influence over stimulus processing. This can be quantified as a function of root mean square (RMS, or the quadratic mean) amplitude of the ongoing waveform and expressed as an Attention Modulation Index, or AMI, (Mishra, Zinni, Bavelier, & Hillyard, 2011):

$$AMI = \frac{(RMS_{attended} - RMS_{ignored})}{(RMS_{attended} + RMS_{ignored})}$$

where

$$RMS = \sqrt{\frac{(x_1^2 + x_2^2 \dots + x_n^2)}{n}}$$

For EEG data, n = (sampling frequency x time in seconds) and x is the voltage measured at each time point sampled.

A higher AMI corresponds to greater top-down modulation, and incorporates both greater amplification of the flicker when attended, and suppression when ignored into a single index. More than one ssVEP frequency can be evoked and recorded at the same time and that the relative amplitude to each frequency reflects covert attention allocation (Morgan et al., 1996). As attention shifts away from one frequency (12 Hz) to another frequency (8 Hz), the AMI to the 12 Hz frequency decreases and the AMI to the 8 Hz frequency increases. Different frequencies stimulate distinct neural networks (Ding, Sperling, & Srinivasan, 2006; Srinivasan, Bibi, & Nunez, 2006) (Bridwell & Srinivasan, 2012) and, importantly for the present study, reflect distinct cognitive aspects of top-down attention control. ssVEPs in lower alpha frequencies reflect networks that suppress ignored stimuli, while ssVEPs in the high-alpha range reflect networks that amplify attended stimuli (Bridwell & Srinivasan, 2012). ssVEPs are also sensitive to anxiogenic manipulation; ssVEP spectral power increases in response to emotional images compared to neutral stimuli (Hajcak, MacNamara, Foti, Ferri, & Keil, 2011; Keil et al., 2011; Moratti, Keil, & Stolarova, 2004; Wieser, McTeague, & Keil, 2011).

While the ssVEP AMI provides a measure of top-down control, at the same time we can use the P3 event related potential (ERP) to measure bottom-up

attentional capture by task-relevant and by task-irrelevant stimuli. The P3 reflects a context updating response, and is generated when stimuli differ in some way from preceding stimuli. The P3 consists of two waveforms. The P3a, or 'novelty P3', is most sensitive to featural differences, and is maximally driven by novelty and salience of unexpected stimuli. The stimulus need not be attended prior to onset; unattended, unexpected and salient stimuli will generate a large P3a irrespective of task-relevance. The P3a originates in frontal structures (Dien, Spencer, & Donchin, 2003) and its maximal deflection is measured at frontal (Fz) and central (Cz) sites along the midline. The P3b, on the other hand, is sensitive to matching an expected but rare stimulus to memory, such as is required in a target detection task. It is maximal over the parietal region (Pz) and localization studies revealed it is most likely generated from the temporo-parietal junction (Dien et al., 2003). It has been used to evaluate workload (Donchin, 1981) and decreases as workload increases and attentional resources are consumed. For more detailed reviews of these well studied waveforms see Polich (2007), Spencer, Dein & Donchin (2001), and for an early account (Donchin, 1981).

Thus, for the purposes of studying attention control, changes in the P3a amplitude should reflect the relative amount of attention captured by task-irrelevant, potentially distracting stimuli. The change in amplitude of the P3b should likewise reflect the relative amount of attention resources devoted to detecting a task relevant target.

The present study examines attention-related ERPs (the P3 and P3b) and ssVEP modulation (AMI) to examine the effects of anxiety (induced by threat of shock) on the persistent direction of attention towards task-relevant and away from task-irrelevant and potentially distracting stimuli. Threat of shock is a reliable and valid (Schmitz & Grillon, 2012) means to induce anticipatory state anxiety for within-subjects designs. If anxiety shifts attention processing away from top-down task-relevant processing in favor of bottom-up stimulus driven systems, salient distractors should elicit a larger P3a as they compete with task-relevant stimuli for processing resources, while P3b amplitude to less inherently salient, but task-relevant targets should decrease. If greater ssVEP modulation reflects efficient attentional control, and anxiety erodes attentional control, individuals should exhibit a smaller difference in ssVEP amplitude (smaller AMI) as state anxiety increases. If ACT's specific prediction that anxiety selectively impairs inhibition to a greater extent than other executive control processes is correct, anxiety-induced differences in AMI should be driven mainly by impaired inhibition of task-irrelevant stimuli, and observed in the suppression-sensitive 8.6Hz ssVEP.

We predict that an inverse relationship exists between one's anxious state and the ability to sustain top-down attentional control and suppression of task-irrelevant stimuli.

- **Under anxiogenic conditions, ssVEP Amplitude Modulation Index (AMI) will decrease as anxiety increases reflecting reduced capacity to selectively filter incoming stimuli.**

Additionally, if anxiety compromises selective attention-directed processing, attention capture by discrete task relevant (target) and task irrelevant (distractor) stimuli should reflect that difference as anxiety increases.

- **Attention-related neural responses to unexpected task-irrelevant stimuli (P3a) will be directly related to induced anxiety reflecting weaker executive inhibitory control against distraction compared to neutral conditions.**
- **Neural responses to expected task-relevant target stimuli (P3b amplitude) will be inversely related to induced anxiety levels reflecting less attention devoted to task-relevant targets.**

Additionally, trait measures of anxiety may predict responses to the threat paradigm. Those with high Trait Anxiety (Spielberger, Gorsuch, & Lushene, 2005) and high Anxiety Sensitivity (Deacon, Abramowitz, Woods, & Tolin, 2003) exhibit notable differences in attention control (Bishop, 2008b; Derryberry & Reed, 2002; Koster et al., 2006; Sehlmeier et al., 2010). Thus, the present study will also examine in an exploratory manner whether trait measures of anxiety (STAI-Trait and ASI) are related to the neural responses measured.

2. Methods

In order to assess the effect of anticipatory anxiety on the balance between top-down and bottom-up attention control mechanisms we recorded Electroencephalography (EEG) under three levels of threat while participants completed a target-detection task. The experiment involved two 1.5-2 hour recording sessions in a dimly lit room. One session was a “Shock Day” (SD) and the other “No-Shock Day”(NSD); these were counterbalanced for order across the two sessions. All participants gave informed consent before filling out a series of questionnaires during the first session. Both sessions occurred at the same time of day for each participant (+/- 1 hour), roughly one week apart (1-14 days).

2.1 Target Detection Task (Figure 2). Two alphanumeric sequences appeared in white on a black background each 9 cm to the left and right of a central fixation cross (19” Dell monitor, 50 cm from the participant’s nose).

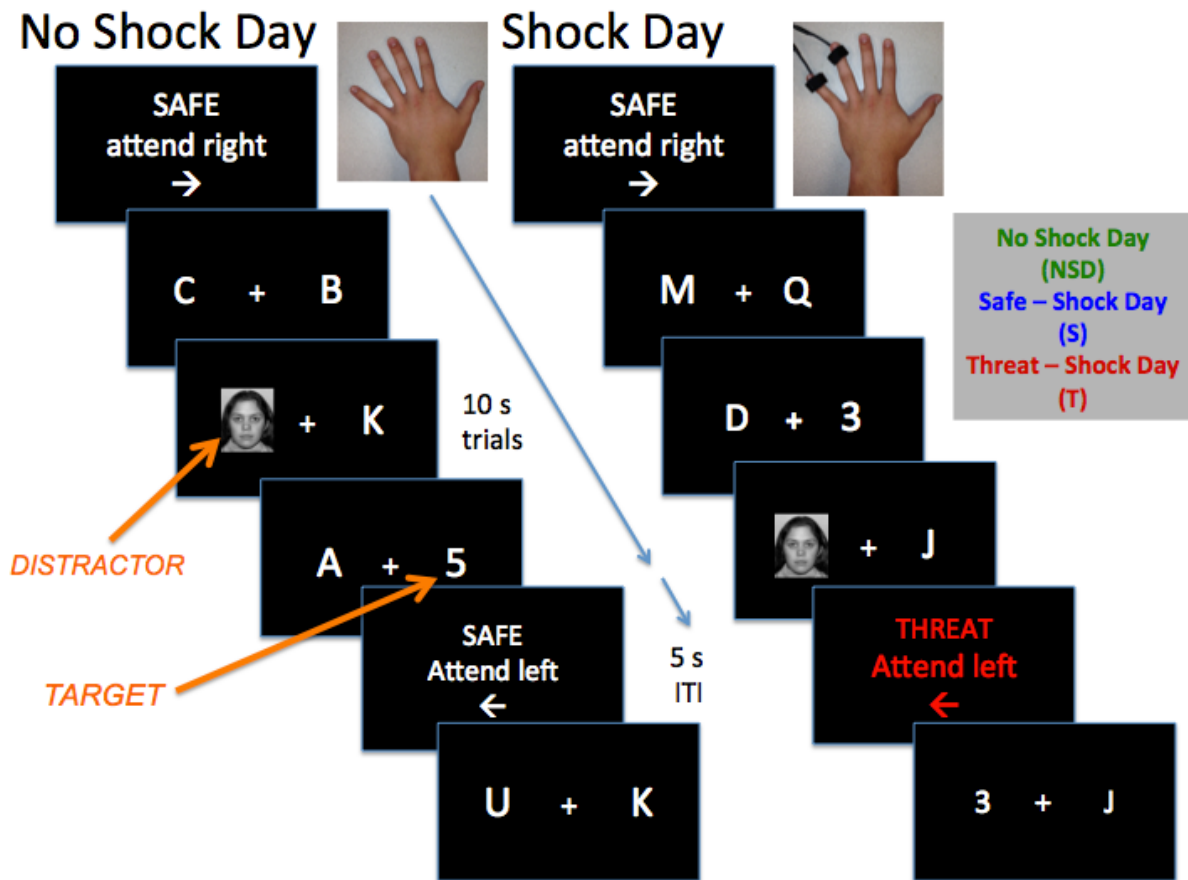


Figure 2: Illustration of task and stimuli paradigm. At the beginning of each trial, participants were instructed to visually fixate on the center cross, but to attend covertly to one side of the screen and press a button – as quickly and accurately as possible – when they saw a digit (target) among a series of letters. A similar stream of letters was presented in the opposite visual field, but instead of digits, neutral faces designed to be distracting, appeared pseudo-randomly. On the No Shock Day, participants performed only Safe trials. On the Shock Day, Safe trials were mixed with Threat trials; participants were at risk of receiving a shock at any time during the Threat trials. The sequences of letters progressed at a speed of 12 Hz on one side and 8.6Hz on the other side (counterbalanced, left and right) and provided the necessary flicker to generate the ssVEP frequencies. ERPs were time-locked to the presentation of the digits (targets) and the faces (distractors) that appeared within the flickered sequence in place of a letter.

Participants focused their gaze on a central fixation cross throughout the duration of each 10-second trial, and *covertly* (without shifting their eyes) attended either the left or right sequence. The objective was to press a button as quickly and accurately after they detected a target (digit) among the letters. One sequence progressed at a rate of 8.6 Hz (letters/second) and the other at 12 Hz; these frequencies were



Figure 3: Example of a neutral face from the NIMSTIM picture set that appeared periodically in the unattended hemifield.

counterbalanced so that each frequency appeared an equal number of times on each side of the screen. The rate at which the letters and target digits appeared was too fast for the digits to be detected if the participant was not actively attending the sequence. No digits appeared in the ignored sequence; rather, to best challenge attention control with salient but task-irrelevant stimuli, we presented neutral faces among the letters as potential distractors (black and white neutral faces, NIMSTIM images 1-42, (Tottenham, 2013)(Figure 4). Since bottom-up systems are more sensitive to salience, the distractor needed be more salient than the target digit. Colored squiggles have exhibited such properties (Courchense, Hillyard, & Galambos, 1975) but faces were chosen as they stimulate preferential processing even when unattended (Vuilleumier, Armony, Driver, & Dolan, 2001). We chose neutral faces (as opposed to emotional expressions) for two reasons: 1) An emotional distractor might have added a confounding emotional load in addition to that imposed by the threat-of-shock,

especially if the expression was negative (see the distinction between “hot” and “cold” stimulus processing in (Robinson et al., 2013)); and 2) anxiety has been linked to diminished distractor inhibition even when no threatening stimuli are present (Bishop, 2008b). Both targets (digits) and distractors (faces) appeared randomly and with the same probability. The task was created and controlled using Presentation® software (Version 0.70, www.neurobs.com) on a desktop PC (Dell, Windows 2007 operating system).

Before starting the first session participants practiced until they were able to perform the task without moving visual gaze from the central fixation cross. Researchers verified compliance and task proficiency before beginning experimental trials and during the testing session by monitoring both the participants’ eyes on a webcam placed above the monitor, and the continuous display of muscular activity recorded from horizontal electrooculogram (HEOG) electrodes.

2.2 Stress manipulation

The Shock Day (SD) included “Threat” trials intermixed with “Safe” trials; the No-Shock Day (NSD) included only “Safe” trials. During the SD participants wore electrodes on the fourth (ring) and fifth (pinky) fingers of the left (non-dominant) hand (see Figure 3) that delivered a mild shock (4mA, 100ms, finger stimulator, Colbourn Instruments), delivered in accordance with standardized safety guidelines (Butterfield, 1975). Participants were at risk at receiving a shock at any point during the Threat trials, but were at no risk of receiving a shock during

Safe trials. The shocks during Threat trials were delivered at random (Grillon, Baas, Lissek, Smith, & Milstein, 2004). An instruction screen indicated whether the subsequent trial would be a “Safe” or “Threat” condition. During the NSD all trials were Safe and participants did not wear the finger electrodes. This resulted in three experimental conditions:

Threat: electrodes attached, risk of shock;

Safe: electrodes attached, no risk of shock; and,

No Shock Day (NSD): electrodes not attached.

These conditions were intended to create three increasing levels of anxiety (NSD < Safe < Threat). Measures taken during the Shock Day trials reflect reactions to the non-specific threatening context, where the participant is aware he or she will be shocked sometime over the course of the 5-minute experimental block. Measures taken during the Threat trials have the addition of an acute, cued threat of shock sometime within an immediate 10-second period.

It is important to note that most shock studies employ a method that allows the participant to choose an amperage level, yet a sense of control is also known to decrease anxiety (Geer, Davison, & Gatchel, 1970). Predictability of shock has also been shown to attenuate anxiety (Schmitz & Grillon, 2012). In light of these observations, and because it is traditionally very difficult to ethically and consistently induce stress in a laboratory setting, we chose instead to use a

standard amperage for all participants (4mA), did not tell them how many shocks would be delivered, and did not deliver sample shocks prior to the first Shock Day Threat trial. Instead, the shock was described as a sensation that most find “extremely uncomfortable, but not painful.” Though the standard level of shock we used was well within OSHA safety standards, previous studies that have also set a standard amperage for all participants set the level below that which we used (for example, 1.8mA in Grillon, Ameli, Woods, Merikangas, & Davis, 1991). Although this suggests our threat-of-shock paradigm is among the most stressful currently in publication, most participants reported the sensation and threat was modestly aversive.

2.3 Measures

Trait Measures & population characteristics. Prior to Session 1, before entering the testing room and before they knew if Session 1 was a Shock Day (SD) or No-shock Day (NSD), participants completed the Spielberger Trait Anxiety Inventory (STAI-T, Spielberger et al., 2005), Anxiety Sensitivity Index (ASI, Deacon et al., 2003), Beck Depression Inventory (BDI, Beck, Steer, & Brown, 1996), and the Fear Survey Schedule II (FSS II, Greer, 1965). The STAI and ASI were used as predictor variables in exploratory hypotheses regarding how trait anxiety interacts with the dependent measures. The BDI and FSS II were included to characterize the population and, because trait anxiety often correlates with depression and fear responses, to assess whether any findings including the STAI and ASI could be driven instead by other closely-related

factors. It has also been demonstrated that Trait Anxiety and Trait Fearfulness have differential lateralization in the brain suggesting different influences on cognitive function (Dien, 1998).

Electroencephalography (EEG), ERPs and ssVEPs. Researchers fitted participants with a 36 active-electrode BrainVision atciCAP system (Brain Products, Munich, Germany). Thirty-two electrodes recorded brain data from the scalp in a standard 10-20 montage (Jasper, 1958). Two electrodes placed above and to the right of the right eye captured horizontal and vertical eye movement, and two additional electrodes below the right eyelid captured startle responses. Impedance thresholds for all electrodes were kept below 7m Ω and all data were recorded at a 1000Hz sampling frequency.

The alphanumeric sequences in the task also generated the 8.6Hz and 12Hz ssVEPs. The digital monitor's 60 Hz refresh rate limited the frequencies at which the sequences could progress reliably; hence a new letter appeared every five frames for the 12Hz sequence and every seven frames for the 8.6 Hz sequence. Likewise, targets (digits) and distractors (faces) presented within the attended and unattended frequencies, respectively, elicited the ERPs of interest.

Manipulation Checks.

Self Report. The State portion of the STAI indicated pre-session stress for both days. During testing sessions participants indicated their current emotional

valence, level of arousal, and sense of control (dominance) using three subscales on the 9-point Self Assessment Manikin (SAM, Bradley & Lang, 1994) and marked a point along each of four 100mm Visual Analog Scales (VAS) to rate how comfortable, calm, relaxed and anxious they felt. Two of the VAS scales oriented the positive end towards the left of the sheet while the other two oriented the positive end towards the right. The VAS and SAM ratings were assessed before (“pre”), half way through (“during”) and after each testing session (“post”). During the Shock Day the “pre” testing assessment occurred just after the electrodes had been placed on the participant’s fingers, and the “post” assessment occurred after the electrodes had been removed.

Startle. The startle blink response increases as anxiety increases (Filion, Dawson, & Schell, 1998) and provides a physiological index of amygdala activation. White noise bursts (100ms, 60DBA against 48DBA ambient noise) triggered startle responses during each type of trial, which indicated whether the stress manipulation (threat of shock) was effective in creating anxiety. Two electrodes positioned on the lower orbis ocularis (active below the pupil, and reference below the outer corner of the eye) recorded the magnitude of startle responses.

2.4 Procedures

The Shock Day (SD) and the No Shock Day (NSD) were counterbalanced for order and across gender. On the first testing day and after giving informed

consent, participants filled out: the Trait portion of the STAI; the ASI; the FSS II; and, the BDI. Researchers then informed the participant whether the first testing day would be the SD or NSD after which participants completed the State portion of the STAI. All of this was done before participants entered the testing room. During the second session participants they only filled out the State portion of the STAI before entering the testing room.

In the testing room researchers placed the EEG cap and eye electrodes while participants practiced the task. During this time researchers also screened participants for a measurable startle response to random white noise bursts presented during the practice trials. Those who did not exhibit a measurable startle did not continue the study and were given \$5. Participants who exhibited measurable startle practiced the task until they were able to detect the targets without shifting their eyes from the central fixation cross.

The testing session consisted of four experimental blocks of 25 trials each with a one to two minutes of rest between blocks. Researchers attached the finger shock electrodes before the first block on the SD. On both days participants completed the Self Assessment Manikin (SAM) and Visual Analog Scales (VAS) before the first block ('before'), again between blocks 2 and 3 ('during'), and after block 4 ('after'). On the SD participants filled out the first SAM and VAS ratings just after the finger electrodes had been attached, and the final SAM and VAS

ratings after the electrodes had been removed. Participants received \$40 for completing both sessions (Figure 4).

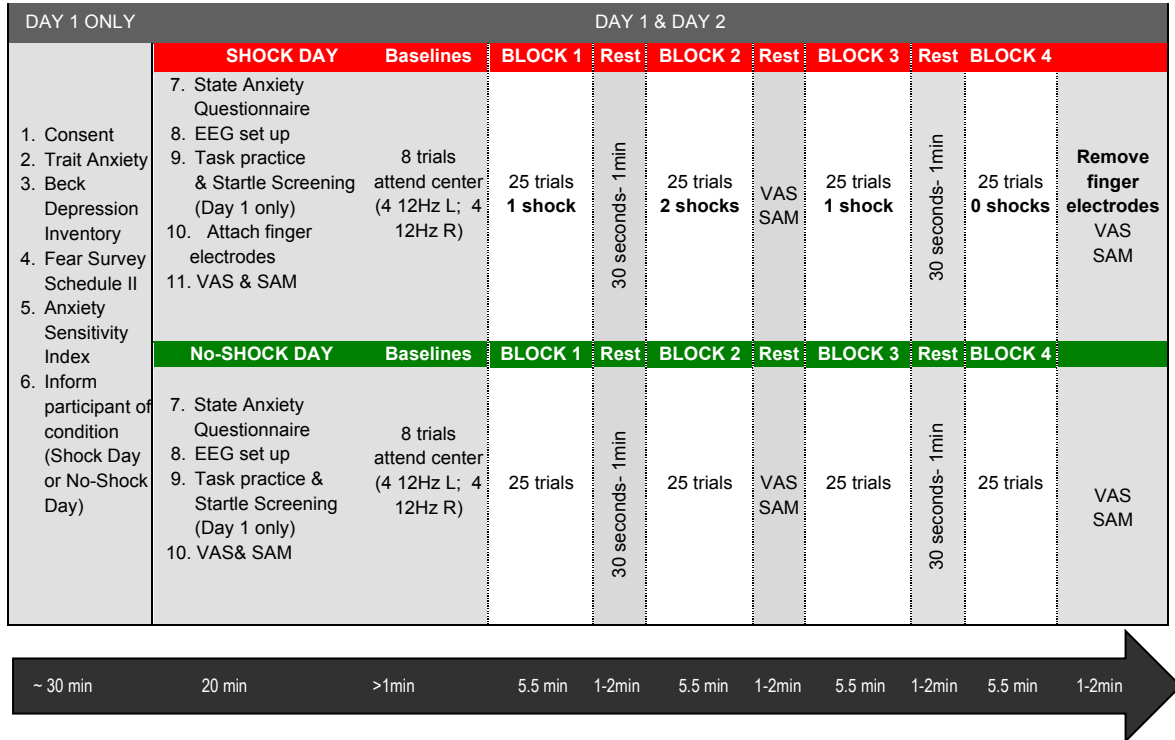


Figure 4. Order of testing procedures from left to right, during the Shock Day (top row) and the No-Shock Day (bottom row). Times listed on the arrow indicate the duration of the testing stage above.

2.5 Signal processing and statistical approach.

Startle. Startle data were processed in accordance with the standards outlined in Blumenthal, 2005 (Blumenthal et al., 2005). Data from the active startle electrode (lower-eyelid, below the pupil) were re-referenced against the outer startle electrode (lower eyelid, below the corner of the eye). Signals were band-pass filtered (28-40Hz with a 4th order Butterworth), rectified, smoothed (FIR Kaiser), visually inspected for non-startle artifact and averaged. Standardized area under the curve was calculated for each participant's data from 50ms-120ms after noiseburst onset for each condition.

Event Related Potentials (ERPs) Signals from all scalp electrodes were referenced on-line to the left ear and were re-referenced off-line to an average recorded from both ears. Data were band pass filtered between 0.1-20 Hz using a 3rd order zero-phase shift Butterworth filter. One-second epochs were extracted from 200 ms prior to stimulus onset to 800 ms after stimulus onset for both target (digit) and distractor (face) stimuli. Each epoch was baseline corrected against the 200 ms pre-stimulus average and epochs distorted by blinks or excessive noise (due to shocks or startle probes) were rejected via visual inspection. The remaining epochs were averaged together to form an ERP for each condition for each person and the grand average for the group.

Peaks of interest in the target and distractor ERPs were identified from the grand average ERPs for the whole sample. The P3b to the target stimulus was maximal at the Pz electrode 466 ms after stimulus onset and averaged over a window 200 ms before and after peak latency. The P3a to the distractor stimulus was much smaller, and its latency was earlier, peaking 360 ms after stimulus onset at Fz; the P3a was averaged over a 50 ms window.

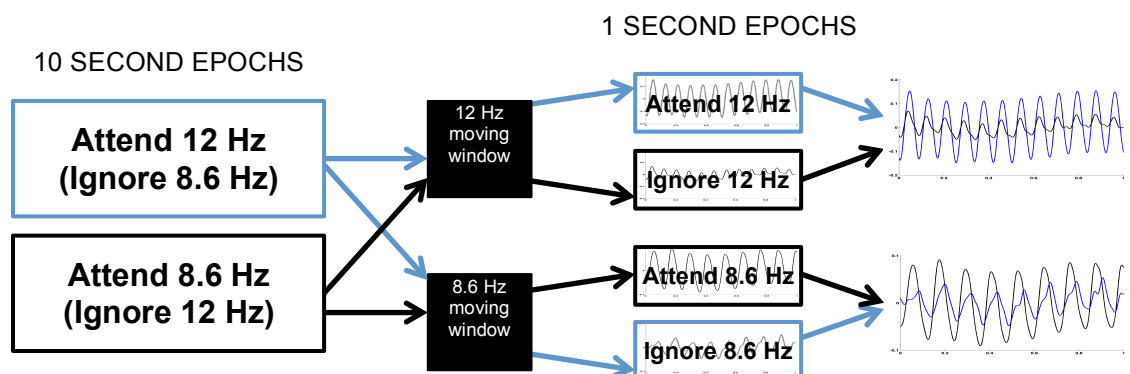


Figure 5. Signal processing to isolate ssVEPs for each condition and frequency.

Steady State Visual Evoked Potentials (ssVEPs): The alphanumeric sequences in the target-detection task were used to generate distinguishable steady-state visually evoked potentials at 8.6Hz and 12Hz. Each 10-second trial epoch was extracted from filtered data and identified as either “Attend 12Hz, Ignore 8.6Hz” or “Attend 8.6Hz, Ignore 12Hz” for each condition. All epochs were averaged using a 1-second moving window average synced with each frequency to create “Attend” and “Ignore” averages for both 12Hz and 8.6Hz signals (see Figure 5).

The resulting 1-second ssVEP averages for each trial were averaged together for Attend and Ignore values for each electrode. Root mean square values were calculated for each electrode and averaged over 10 electrode sites (P3, P4, P7, P8, TP9, TP10, PO9, PO10, O1, O2) (Mishra et al., 2011). From these averaged RMS values we calculated the Attention Modulation Index (AMI, equation presented in the Introduction) for each condition.

Statistical Approach: The STAI-S scores were tested using a two-tailed t-test. State measures assessed before, during and after each session (VAS and SAM scores) were entered into a 2 (No-Shock Day, Shock Day) X 3 (before, during, after) repeated measures ANOVA (RMANOVA). All other measures (startle, performance, ssVEP AMI scores, and ERP amplitudes) were standardized when appropriate and entered into a one-way, three level ANOVA for condition (NSD, Safe, Threat). In instances where data violated the sphericity assumption, Greenhouse-Geisser adjusted degrees of freedom were used to control for Type I error, though the adjustments did not change the results in any of the tests reported herein. Post-hoc pairwise comparisons were corrected using Tukey's HSD post hoc analysis.

3. Results

3.1 Sample characteristics. Fifty-five college-age participants read and signed the consent form; three lacked a measurable startle response and were not enrolled. No participants declined to participate after the shock condition was described and no participants requested to discontinue the experiment after experiencing shock. The EEG data from two participants were rejected for excess eye blink artifact. The remaining behavioral and self-report data consisted of N =52 (26 m) participants, and EEG sample included N = 50 (25 m) participants.

Table 1. Characteristics of the Sample. Means and standard deviations of the sample and normalized data from comparable populations.

MEASURE	Mean(SD)	Normed Samples
Spielberger Trait Anxiety (STAI-T)	Total: 34.81 (6.91) Male: 35.22 (7.15) Female:34.36(6.75)	College age adults Male: 36.47(10.02) Female: 38.76(11.95) (Spielberger et al., 2005)
Anxiety Sensitivity Index (ASI)	Total: 14.11 (8.17) Male: 14.69(8.15) Female: 13.48(8.31)	Healthy adults Male: 15.4 (8.1) Female: 23.6 (10.9) (Reiss, Peterson, Gursky, & McNally, 1986)
Beck Depression Inventory (BDI)	Total: 3.58 (2.94) Male: 3.63(3.27) Female: 3.52(2.6)	0-13 “minimal depression” (Beck et al., 1996)
Fear Survey Schedule (FSS)	Total: 129.06 (32.8) Male 128.04(37.13) Female: 130.16(28.1)	College age adults Total:98.64(38.47) Male: 81.81(33.64) Female: 108.47(36.78) (Bernstein & Allen, 1969)

3.2 Assessment of State Anxiety

The Spielberger State Anxiety Inventory. STAI-S scores were significantly greater at the beginning of the Shock Day session than before the No Shock Day (NSD) session. $State_{SD} = 29.54(\text{SEM} = 0.99)$, $State_{NSD} = 33.73(\text{SEM} = 1.26)$, $t_{(51)} = 3.44$, $p = .001$, 2-tailed).

Self-Assessment Manikin (SAM). Higher scores on the total SAM score and on each of the subscales indicate more negative states. All omnibus tests for each SAM subscale were significant such that valence became more unpleasant, arousal increased and dominance/control decreased to a greater degree during the Shock Day (compared to before and after testing) than they did on the NSD (Emotion: $F_{(2,100)} = 5.00$, $p = .009$; Arousal: $F_{(2,100)} = 4.59$, $p = .012$; Dominance/Control: $F_{(2,100)} = 17.84$, $p < .001$). Participants reported more negative emotion, greater arousal and less dominance/control during the Shock Day compared to the NSD (Day main effect Emotion: $F_{(1,50)} = 6.32$, $p = .015$; Arousal: $F_{(1,50)} = 34.69$, $p < .001$; Dominance/Control: $F_{(1,50)} = 15.98$, $p < .001$) and during the testing session compared to before or after the testing sessions (Time main effect, Emotion: $F_{(2,100)} = 20.15$, $p < .001$; Arousal: $F_{(2,100)} = 4.91$, $p = .012$; Dominance/Control: $F_{(2,100)} = 20.85$, $p < .001$) (Figure 6).

Self Assessment Manikin (SAM)

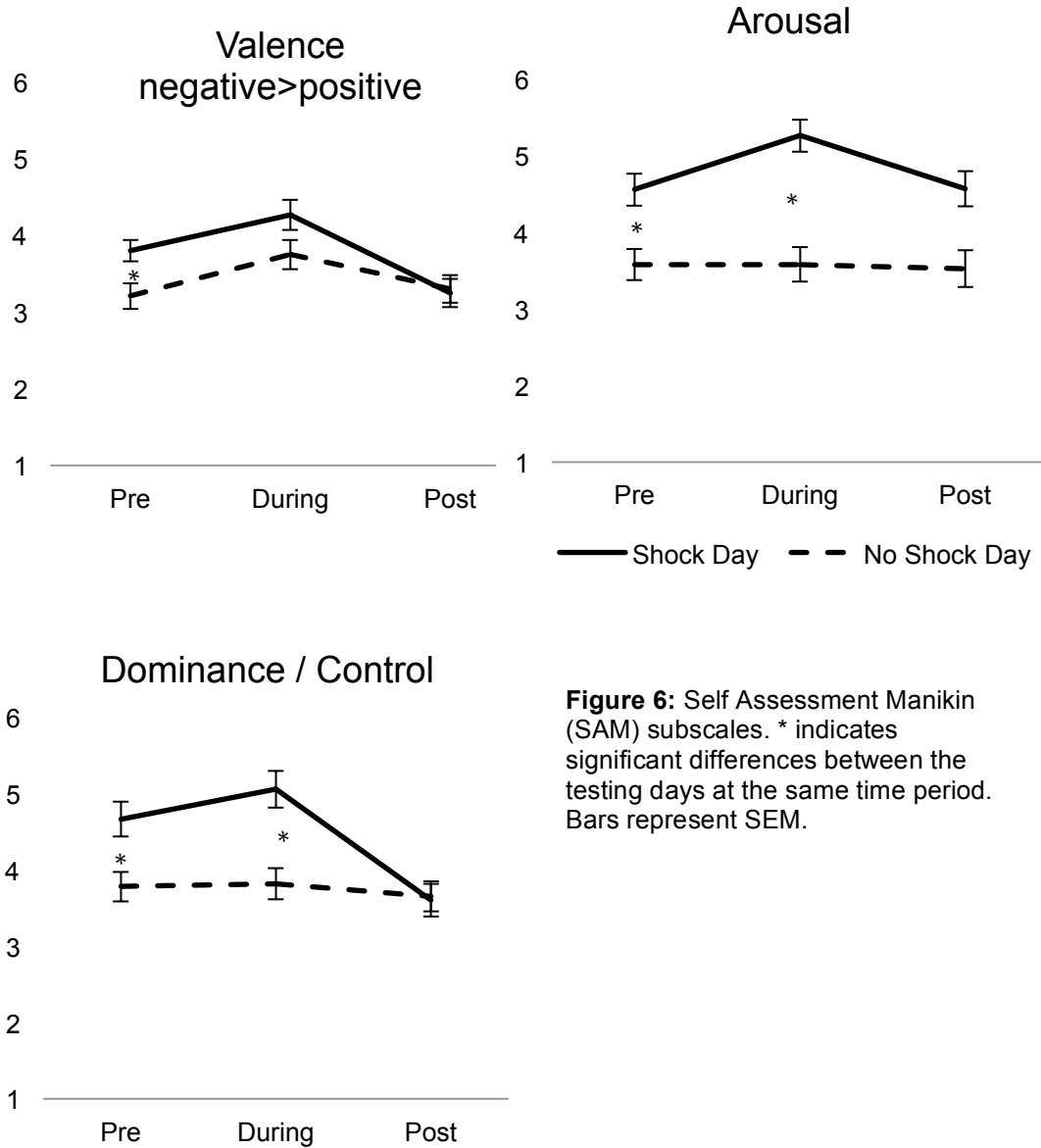


Figure 6: Self Assessment Manikin (SAM) subscales. * indicates significant differences between the testing days at the same time period. Bars represent SEM.

Visual Analog Scales. Participants reported feeling a significantly greater increase in anxiety (“*How anxious am I?*”) and greater decrease in feeling calm (“*How calm am I?*”) and relaxed (“*How relaxed am I?*”) during the testing session compared to before and after the session on the Shock Day than they did on the

NSD (anxiety interaction: $F_{(2,102)} = 10.27$, $p < .001$; calm interaction: ($F_{(2,102)} = 7.02$, $p = .002$); relaxed interaction: $F_{(2,102)} = 6.35$, $p = .004$). While the interaction was not significant for self-reported discomfort (“How uncomfortable am I?”) participants showed significant main effects for Day (NSD vs Shock Day) and for Time (Pre, During, Post) for all four VAS question. Participants reported feeling greater overall anxiety and discomfort and feeling less calm and relaxed on the Shock Day compared to the NSD (main effect for Day for anxiety: $F_{(1,51)} = 38.63$, $p < .001$; discomfort: Day $F_{(1,51)} = 15.17$, $p < .001$; calm: $F_{(1,51)} = 15.17$, $p < .001$); and feeling relaxed: $F_{(1,51)} = 30.62$, $p < .001$). They also all showed greatest feelings of anxiety, discomfort and the least amount of calm and of feeling relaxed during the testing session compared to before and after the session (anxiety: $F_{(2,102)} = 23.06$, $p < .001$; discomfort: $F_{(2,102)} = 8.92$, $p < .001$; calm: $F_{(2,102)} = 12.85$, $p < .001$; and feeling relaxed: $F_{(2,102)} = 12.84$, $p < .001$).

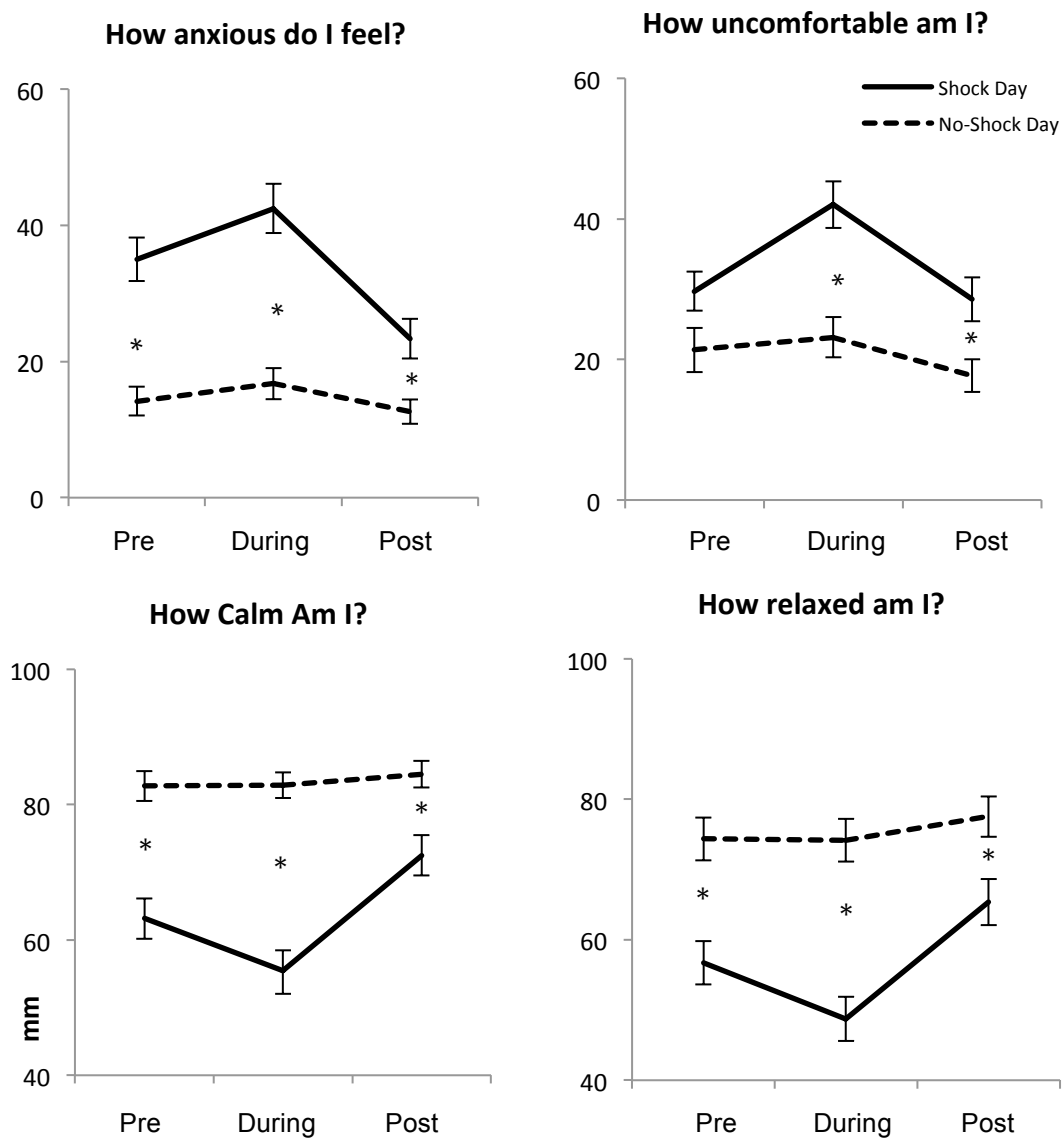


Figure 7. Visual Analog Scales. * indicates significant differences between the same time point (Pre, During, Post) on each measure.

Startle. As depicted in Figure 8, the threat protocol reliably potentiated startle across the three conditions ($F_{(2, 48)} = 48.28, p < .001$). Startle for the Threat condition was larger than the Safe condition ($\text{Startle}_{\text{Threat}} - \text{Startle}_{\text{Safe}} = 0.408, p < .001$), and both were larger than the startle on the No Shock Day ($\text{Startle}_{\text{Threat}} - \text{Startle}_{\text{NSD}} = 0.467, p < .001$; $\text{Startle}_{\text{Safe}} - \text{Startle}_{\text{NSD}} = 0.069, p = .029$). Average standardized area under the curve (50-150ms after noiseburst) and average peak amplitude values are reported in Table 2.

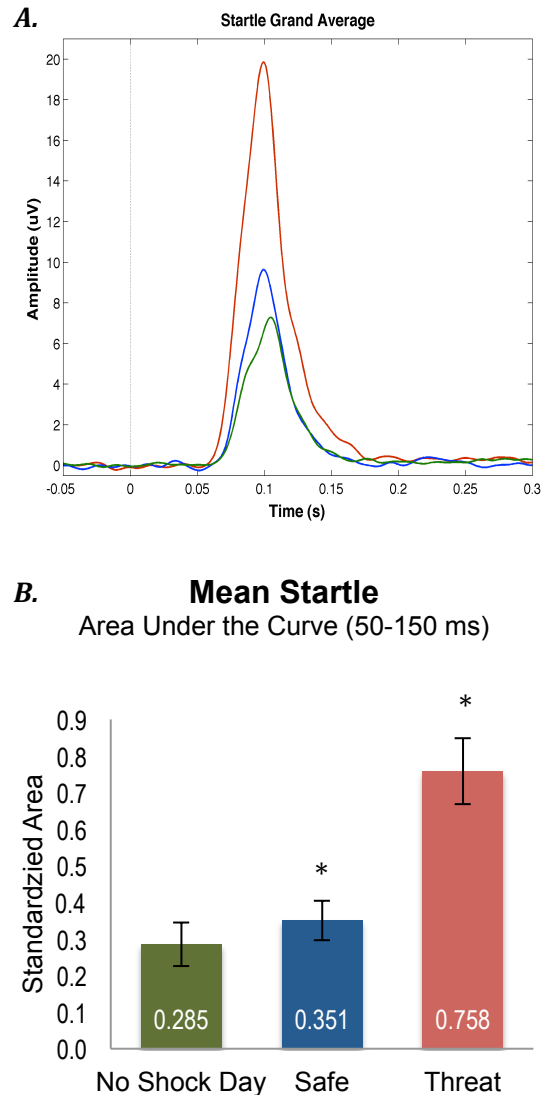


Figure 8. **A.** Startle waveforms for each condition. **B.** Mean standardized area under the curve values for each condition. Error bars represent standardized error, and * indicates significant difference compared to the NSD condition.

Table 2. Standardized and unstandardized values for startle magnitude (standard error) by condition.

Condition	Mean Standardized Area Under the Curve (SE)	Mean Peak Amplitude (SE)
No Shock Day (NSD)	0.285 (.059)	10.31 (1.93)
Safe (S)	0.351 (.054)	14.02(1.87)
Threat (T)	0.758 (.090)	26.71(2.73)

3.3 Dependent Measures

Performance. Reaction times to targets slowed as anxiety increased ($F_{(2,98)} = 7.72, p = .003, \epsilon^2 = .138$). Corrected pairwise comparisons revealed that reaction time during the Threat condition was significantly slower than both the Safe ($RT_{\text{Threat}} - RT_{\text{Safe}} = .012 \text{ s}, p < .001$) and NSD conditions ($RT_{\text{Threat}} - RT_{\text{NSD}} = .012 \text{ s}, p = .012$). Participants showed no significant differences in accuracy between the three experimental conditions ($F_{(2,98)} = .279, p = .7089, \epsilon^2 = .006$).

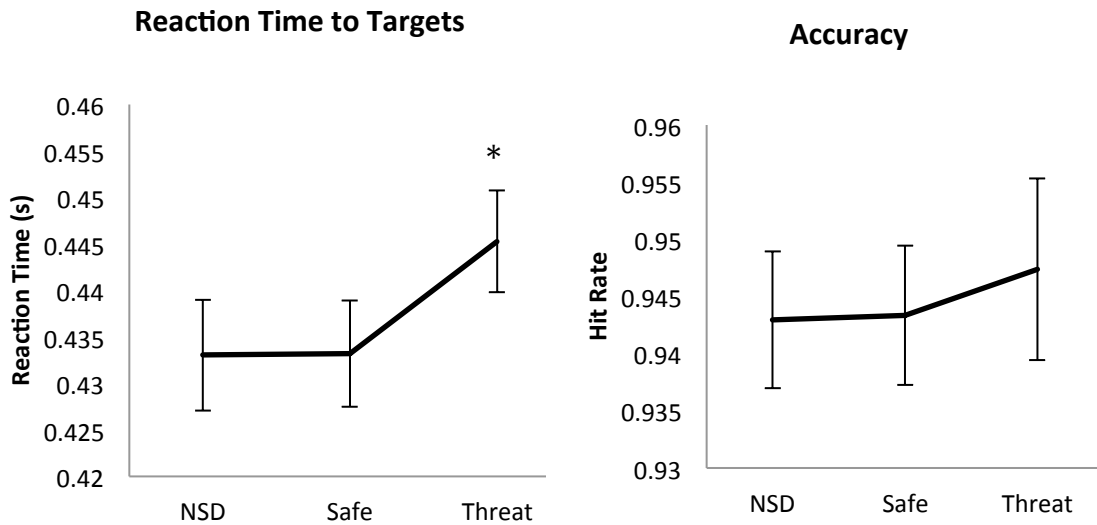


Figure 9. Performance on the target detection task. * indicates significant difference compared to NSD.

ERPs.

P3b. As predicted, the magnitude of the neural response to the target digits was reduced as anxiety increased, reflecting fewer resources were devoted to goal-oriented stimulus processing (Figure 10A; $F_{(2,98)} = 4.48$, $p = .014$, $\epsilon^2 = .084$). Specifically, the P3b amplitude at Pz to the target digits was significantly attenuated in the Threat condition compared to the Safe and No-Shock Day conditions (Figure 10B; $P3b_{NSD} - P3b_{Threat} = 1.622 \mu V$, $p = .045$; $P3b_{Safe} - P3b_{Threat} = 1.711 \mu V$, $p = .037$).

P3a. Contrary to prediction, the magnitude of neural response to the irrelevant faces (P3a amplitude) did not change across condition ($F_{(2,98)} = .819$, $p = .416$, $\epsilon^2 = .016$), indicating there was not a significant increase in attention captured by the task-irrelevant stimuli as anxiety increased. See Appendix 1 for ERP waveforms at each scalp site.

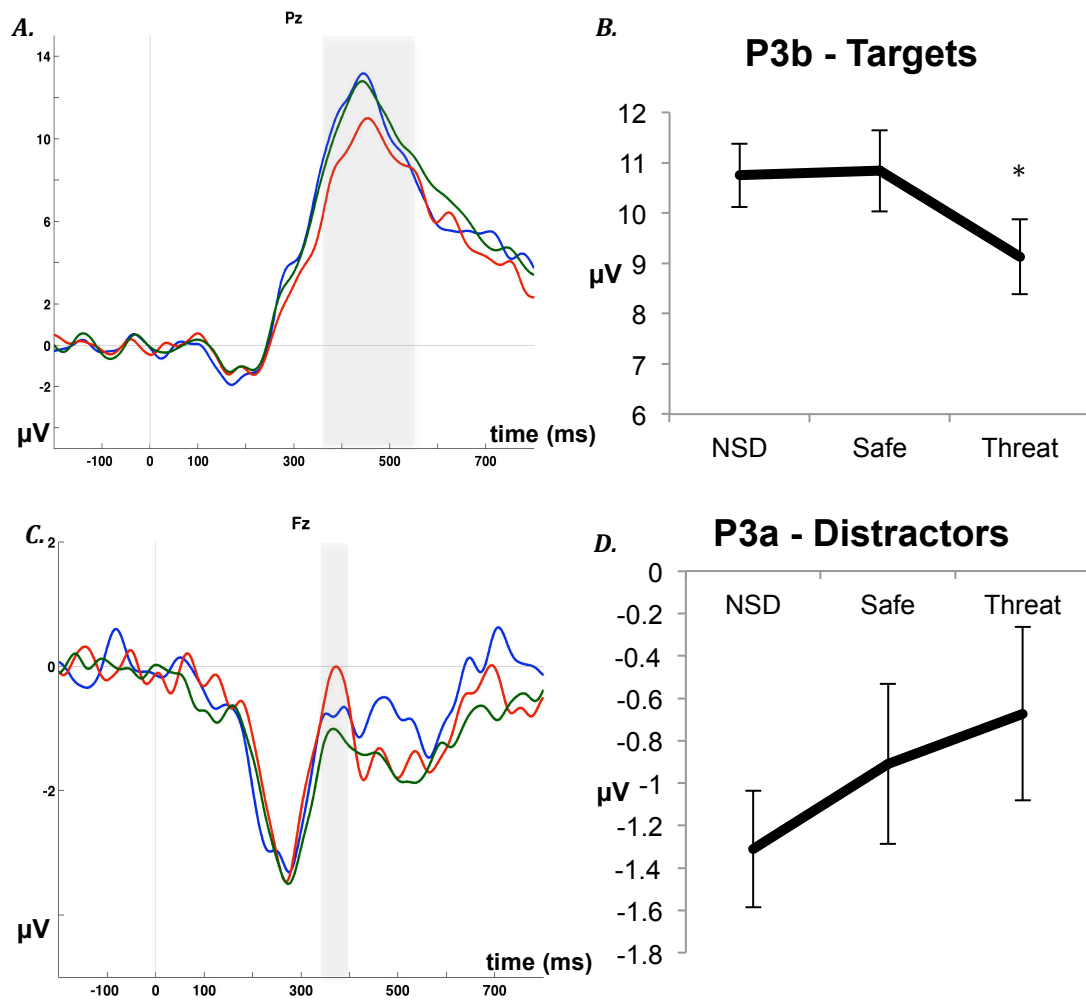


Figure 10. **A.** Grand average P3b waveforms to targets for each condition at Pz. **B.** P3b amplitude (mean area, 346-546 ms after stimulus onset) by condition. **C.** Grand average P3a waveforms to distractors for each condition. **D.** P3a amplitude (335-415 ms after stimulus onset) by condition. For panels A and C, Green line = NSD; Blue line = Safe; Red line = Threat. See Appendix 1 for additional figures. * indicates significant difference compared to NSD condition. Bars represent SEM.

To investigate whether the decrease in P3b to targets was behaviorally relevant, we correlated the difference in reaction times between the NSD and Threat condition with the difference in P3b amplitude between the NSD and Threat condition. The correlation was significant (2-tailed test, $r = .285$, $p = .045$, $R^2 = .081$) indicating that the more anxiety compromised the neural response to the target, the more reaction time slowed in response to the targets.

ssVEPs. Contrary to prediction, participants showed a significant *increase* in the 12 Hz Attention Modulation Index (AMI) as threat increased ($F_{(2,98)} = 4.962$, $p = .009$, $\epsilon^2 = .092$). Corrected pairwise comparisons revealed as significant difference between the Safe and NSD ($AMI_{12NSD} - AMI_{12Safe} = -.041$, $p = .040$) and the Threat and NSD conditions ($AMI_{12NSD} - AMI_{12Threat} = -.041$, $p = .013$). There was no change in the 8.6 Hz ssVEP ($F_{(2,98)} = .098$, $p = .907$, $\epsilon^2 = .002$). This suggests top-down attention engaged under anxiogenic conditions (Safe and Threat) to modulate the 12 Hz frequency. The modulation of 8.6 Hz showed a relatively constant level of modulation over the three conditions.

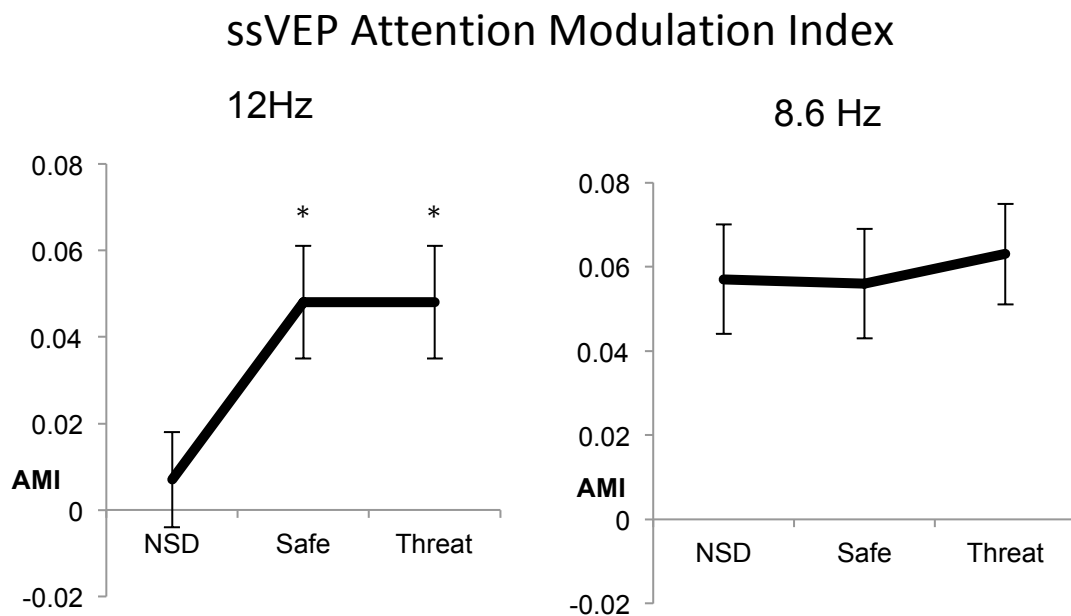


Figure 11. AMI of 12Hz and 8.6Hz ssVEPs. The 12Hz ssVEP shows an increased in modulation during Safe and Threat trials reflecting greater selective filtering as anxiety increases. Modulation of the 8.6Hz ssVEP did not change as a function of anxiety. * indicates significantly different from NSD condition.

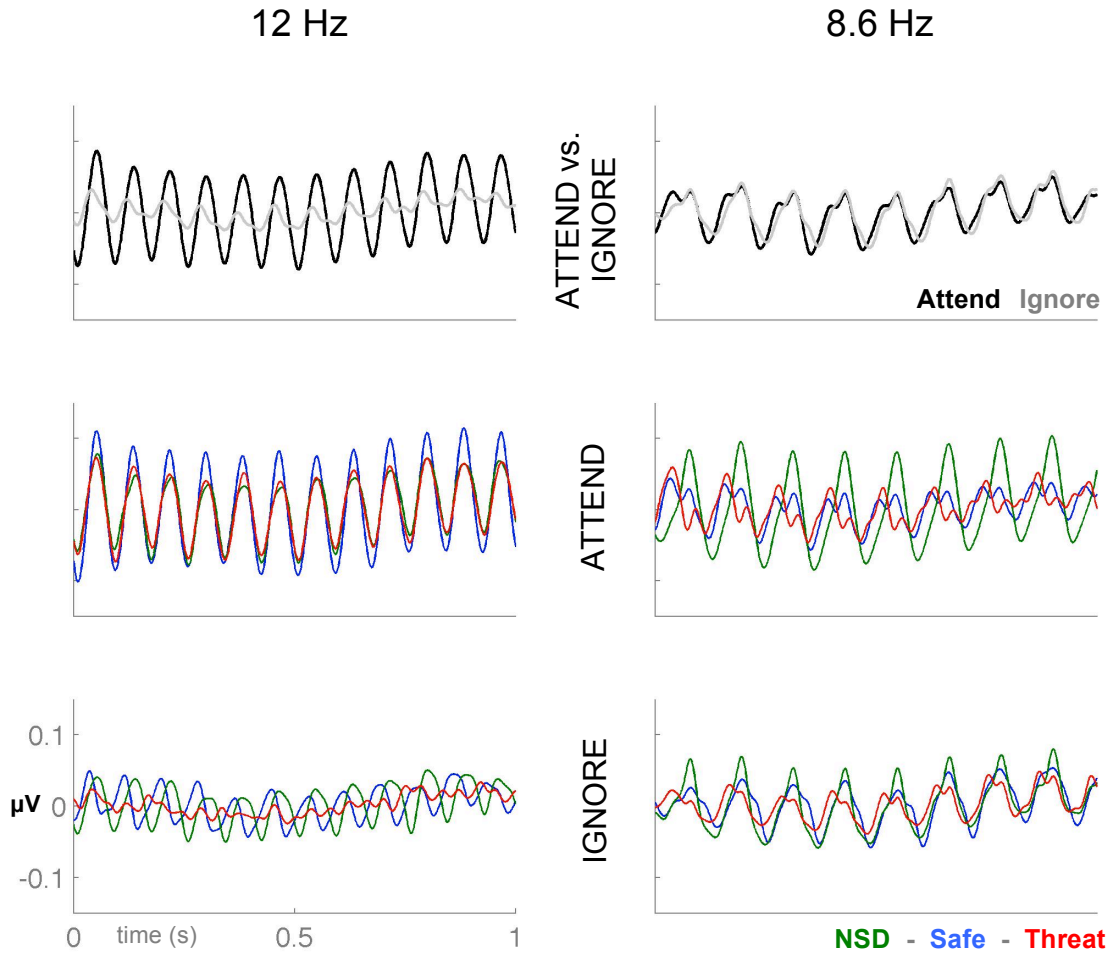


Figure 12. Averaged ssVEP waveforms. **Left column:** 12Hz , **Right column:** 8.6 Hz. **Top row:** $ssVEP_{Attend}$ and $ssVEP_{Ignore}$ for each frequency. Black line: attend, gray line: ignore. **Middle row:** $ssVEP_{Attend}$ for each condition and frequency. **Bottom row:** $ssVEP_{Ignore}$ for each condition and frequency. Green line: NSD, blue line: Safe, red line: Threat.

These results were somewhat surprising. Since AMI is a function of both amplification of the attended signal and suppression of the ignored signal, we examined which of these functions (attend or ignore) was most affected by the threat manipulation. In an exploratory way we entered the 12Hz RMS_{attend} and RMS_{ignore} values into a 3 (condition) X 2 (attend/ignore) ANOVA. The omnibus test was significant for an interaction ($F_{(2,92)} = 3.76, p = .032, \epsilon^2 = .071$) indicating

the anxiety manipulation affected RMS_{attend} and RMS_{ignore} differently; RMS_{attend} amplitude increased while RMS_{ignore} amplitude stayed relatively stable but exhibited a downward pattern (see Figure 13). While neither corrected pairwise comparison (between $RMS_{attend-NSD}$ and $RMS_{attend-Threat}$; nor between $RMS_{ignore-NSD}$ and $RMS_{ignore-Threat}$) was significant, the patterns suggest that both amplification of the attended signal and slight suppression of the ignored signal contributed to the significant difference in AMI between conditions. During the NSD there appears to have been no modulation of the 12Hz frequency: the AMI value is close to zero (and standard error includes zero), and error distributions for 12Hz $RMS_{NSDattend}$ and 12Hz $RMS_{NSDignore}$ overlap suggesting an absence of any top-down filtering of the 12Hz frequency during the NSD. A similar analysis of the 8.6Hz ssVEP showed no interaction, in that neither RMS_{attend} nor RMS_{ignore} seem to have been affected by the anxiety manipulation. Rather there was a marked stability in amplitude for 8.6Hz RMS_{attend} and 8.6Hz RMS_{ignore} even during the NSD.

RMS Amplitude

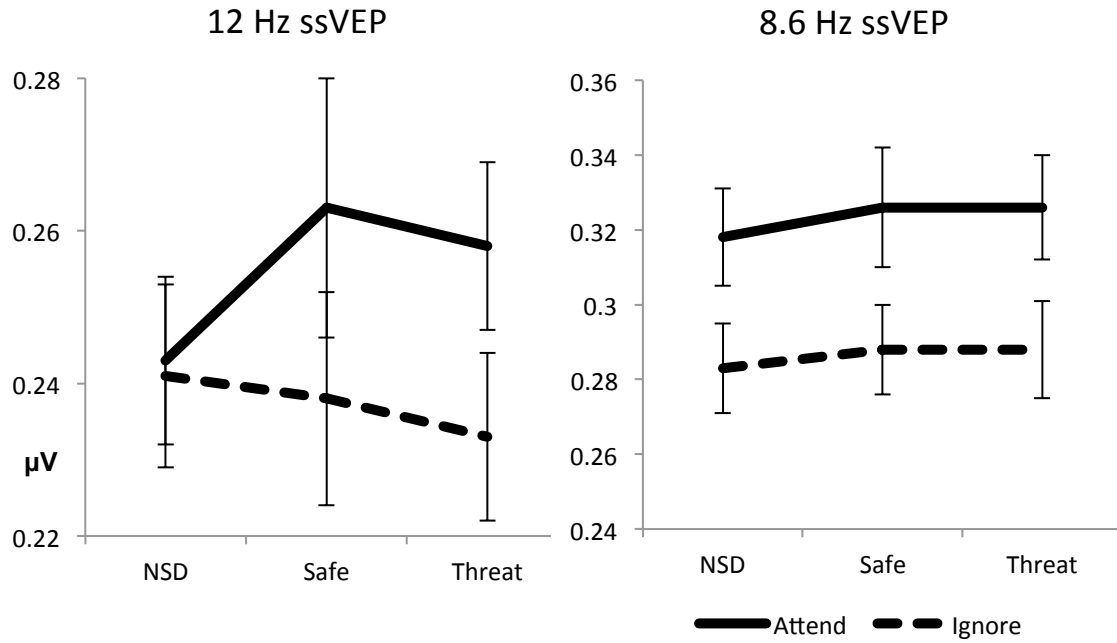


Figure 13. RMS amplitude of ssVEPs. A. 12 Hz RMS_{Attend} increased indicating initial increases in threat increased of the and RMS_{Ignore} decreased as threat increases. B. The 8.6Hz RMS_{Attend} and RMS_{Ignore} stay relatively stable across conditions. Bars indicate SEM.

4. Discussion

The present study examined top-down and bottom-up measures of attention in a single protocol to investigate how these systems compete for limited resources under anxiogenic conditions. Our findings suggest top-down control, as measured by increased ssVEP modulation, responds to moderate increases in anxiety (i.e. Safe trials on the Shock Day compared to the No Shock Day) by selectively amplifying signals from task-relevant stimuli in visual processing areas. Under more intense anxiety however (i.e. Threat trials), neural responses to task-relevant targets diminished and reaction times slowed indicating the top-down control was not sufficient to prevent inefficient allocation of attentional resources. In some cases the findings were different than predicted (ssVEP and P3a results), however the overall pattern of results offers meaningful insight into the dynamics between top-down and bottom-up attentional systems under heightened anxiety. Specifically: 1) The results support the general idea that anxiety impairs the efficiency of attention control. Closer examination of the data also show 2) suboptimal resource allocation was *not* the result of an erosion in top-down control mechanisms, but is more likely the result of cognitive load-related conflict for limited processing resources, and 3) predictions that anxiety selectively compromises executive inhibition of potentially distracting stimuli was not supported. The specific bases for these conclusions are discussed in detail below.

Self-report, startle and performance data indicate that the threat manipulation successfully increased anxiety across the three experimental conditions. Startle potentiation indicated there was a modest increase in anxiety during the Safe trials compared to No-shock Day (NSD) trials, but this increase did not affect performance. Startle potentiation between the Threat trials and NSD trials, however, was six times larger than the potentiation associated with Safe trials, indicating a far greater increase in amygdala activation associated with the immediate cued threat of shock compared to a more general and contextual threat of shock. The larger increase in anxiety during the Threat condition was enough to affect performance; reaction times to targets were slower under the threat condition.

The increase in 12Hz ssVEP AMI was the only dependent measure that changed with respect to the slightly anxiogenic Safe condition. During the more anxiogenic Threat trials, performance slowed and the neural response to targets (P3b) decreased. Yet, there was no further change in ssVEP AMI beyond that observed in response to the Safe trials. This suggests top-down mechanisms engaged in response to the contextual threat (Safe trials), but as anxiety continued to increase the filtering was not enough to prevent degraded processing of targets.

Anxiety reduced the efficiency of cognitive resource allocation and performance. Together, these findings support ACT's primary hypothesis that anxiety reduces efficiency of attention control (and subsequent performance) but not necessarily effectiveness. First, while task accuracy (i.e., effectiveness) did not change as anxiety increased, reaction times slowed. Second, executive-driven top-down filtering mechanisms increased as anxiety increased. There was very little (if any) modulation of the 12Hz ssVEP during the NSD trials, meaning participants did not need to engage top-down filtering mechanisms to the 12Hz flicker to perform the task in the absence of threat, but as anxiety increased so did top-down filtering of the 12 Hz signal. An increase in top-down filtering during the Safe and Threat conditions implies additional effort was required to maintain the same level of performance as in the NSD conditions. Third, spectral analysis of these data elsewhere (see Paper 1) show significant desynchrony in high-alpha power during Threat trials compared to Safe and NSD trials. High-alpha desynchrony is associated with task-related cortical activation, therefore anxiety-induced cortical activity to achieve the same level of task accuracy, thereby reducing efficiency. Likewise, because high-alpha power desynchronized during the same conditions in which we observed smaller P3b amplitude and slower RTs (i.e., only during Threat trials), it is likely the increase in cortical activation reflects some aspect related to inefficient maintenance of attention to maintain performance.

These findings are important as processing inefficiency has a distinct cost in terms of performance. First, while inefficient performers may be able to initially compensate, they are less likely to be able to sustain that performance over time compared to an efficient performer. Secondly, if inefficient performance means there is a relative increase in task-irrelevant cortical “noise” processing in the central executive, that noise may likewise degrade psychomotor efficiency. Psychomotor efficiency is a hallmark of expert performers (such as marksmen) and is associated with less relative cortical activity than that observed in a novice when performing a skilled task (Deeny, Haufler, Saffer, & Hatfield, 2009). Greater relative cortical activity in novices is attributed to non-essential processes that can introduce noise into circuits. Such noise can affect motor control and manifest in jerky kinematics (Deeny et al., 2009, Causer et al., 2011). Cortical efficiency reflects refined processes, which leads to refined motor control. If increased anxiety reduces processing efficiency, it may likewise introduce noise into psychomotor circuits; such noise may not affect simple motor skills like the simple button press in the present study, but could impair the quality of more complex motor skills such as in sharp shooting.

Inefficient allocation of processing resources was not the result of reduced top-down control. ssVEP modulation followed a pattern opposite to that predicted. Though it was expected ssVEP AMI would reduce as anxiety increased, and that this reduction would correspond to the suboptimal deployment of processing resources, we observed a very different, but

illuminating pattern. Rather, ssVEP modulation *increased* in response to moderate anxiety and exhibited no further alteration under more acute and intense threat, while cortical activation increased, neural responses to task-relevant targets decreased, and reaction times lagged. Thus, contrary to ACT's position that anxiety erodes attention control, which then leads to inefficiencies in cognitive processing, we observed a decrease in processing efficiency (as described above) under the highest levels of threat, *without a corresponding lapse in top-down control*. Indeed, top-down control was relatively higher during the highest level of threat (during Threat trials) than it was during the least amount of threat (during NSD trials). Thus, our findings do not support the direct causal links in ACT's model.

Due to the limitations of the present study, we can only speculate as to what might better explain these data. One possibility is that narrowed top-down filtering of bottom-up stimuli may be a response to, rather than the source of, the mechanism responsible for anxiety-induced distractibility. Indeed, there is considerable evidence that anxiety enhances stimulus-driven attention processes (Cornwell, Mueller, Kaplan, Grillon & Ernst, 2012, Cornwell et al., 2011) and lowers the threshold for stimulus detection, improves performance on discrimination and detection tasks (Cornwell et al., 2007; Robinson et al., 2011). Robinson et al. (2013) recently reviewed this literature and summarized their collective findings nicely:

“Specifically, threat of shock studies point to enhanced sensory-perceptual processing across multiple stimulus modalities as a function of anxiety... These findings point to a fundamental shift whereby sensory-perceptual systems are dynamically reconfigured during anxiety states to be more sensitive to sensory perturbations.”

- Robinson et al., 2011

It follows that increased sensitivity to sensory stimuli (bottom-up processing) could ‘overload’ sensory systems (Robinson et al., 2011) and increase conflict for attention. Thus, the attenuated P3b may have been the result of load-related conflict for limited processing resources, rather than the result of reduced top-down control. This latter interpretation would mean these findings lend support instead to the “dual competition” framework for understanding attention and anxiety (Pessoa, 2009).

The general finding that anxiety increases the sensitivity of bottom-up stimuli, also predicts salience will drive processing to a greater degree than task-relevance. From this we would expect to see a relative increase in response to salient distractors, yet we did not observe any difference in the P3a to distractors. While the reduced amplitude of the P3b, and the lack of change in the P3a could mean the salient distractors had processing priority over less salient target stimuli when resources were scarce, such an interpretation speculates beyond the limits

of the current study. Mainly, P3a and P3b have different origins and reflect slightly different stages in bottom-up attention capture mechanism, so it is difficult to compare them directly. Indeed, another speculative interpretation for the same result could be that the conflict for resources occurred *after* the initial attentional recognition of a deviant stimulus (P3a). According to Polich's model (Polich, 2007), incoming stimuli interact and compete for working memory resources after the P3a is generated. If Polich's model is correct, the P3b, which occurs slightly later than the P3a and is related to matching stimuli to working memory, would reflect a conflict for limited processing whereas the P3a might not. The present findings, however cannot offer any additional clarity on this point because ACT also predicts a larger P3a with increased state anxiety.

Speculation of alternate explanations aside, the observation of an attenuated P3b in spite of continued and persistent top-down control as indexed by the ssVEP does not support ACT's hypothesis that the cause of increased inefficiency is due to an erosion of attentional control.

Top-down inhibition was not compromised as anxiety increased. One of ACT's specific contributions to competing theories of anxiety and attention is that it predicts anxiety impairs the efficiency of executive *inhibitory* functions (Derakshan & Eysenck, 2009). However, when we examined the ssVEP data more closely, we found no evidence to support this prediction. First, subcomponents of the ssVEP AMI index (RMS_{Attend} and RMS_{Ignore}) provide

independent information for top-down amplification of task-relevant stimuli (RMS_{Attend}) and for top-down inhibition of task-irrelevant stimuli (RMS_{Ignore}). If anxiety impairs executive inhibition, as anxiety increased the amplitude of the RMS_{Ignore} signal should have also increased. We observed this pattern in neither of the ssVEP frequencies. Rather RMS_{Ignore} amplitudes to both frequencies stayed relatively stable across all conditions. Second, ssVEPs in the high-alpha range (12Hz) tag neural populations primarily involved in top-down amplification of attended stimuli, whereas ssVEPs in the low alpha range (8.6Hz) tag networks mostly involved in top-down suppression of task-irrelevant stimuli (Buschman & Miller, 2007). We also observed top-down amplification that was specific to the 12Hz ssVEP, but we saw no corresponding suppression in the 8.6Hz ssVEP. Instead, the 8.6Hz ssVEP and its subcomponents (RMS_{Attend} and RMS_{Ignore}) were remarkably stable across all three conditions. Additionally, and as mentioned earlier, the P3a to distractors did not indicate that distractors captured attentional resources during anxious compared to non-anxious conditions. Even though resources devoted to task-relevant stimuli were eroded indicating compromised and inefficient attentional processing, these findings do not suggest that it was the result of eroded inhibitory control.

The divergent findings with respect to the selective inhibition of task-irrelevant stimuli in the present study, and enhanced costs associated with inhibition in anti-saccade tasks often cited as supporting evidence for ACT, may be partly due to a lack of specificity in terms. Eysenck and Derakshan refer to general executive

inhibition as preventing disruption of potentially distracting stimuli, and cite studies involving the inhibition of a reflexive response (saccade generation). But the responses are to stimuli that have already captured a certain amount of attention to generate the response in the first place. The findings of the present study on the other hand, are specific to a form of executive *perceptual* inhibition of potentially distracting stimuli in processing stages that precede saccade generation, and in this case, that occurred in the absence of gaze shifts. It may be the case that the fundamental differences between these types of inhibition reflect different stages of the attention control process, and that each could then be differentially affected by anxiety. If this is this case ACT may be refined to better account for such findings.

It is important to note, that the above conclusions are limited by the possibility that ssVEP frequencies not tested in the current study may exhibit the patterns predicted by ACT. Both Buschman and Miller (2007) and Ding et al., (2006) found that different frequencies tag distinct networks and that these networks are distinctly associated with different cognitive functions. Thus, the interpretation of our results remains limited to the frequencies tested.

In summary, the results of the present study support ACT's hypothesis that anxiety decreases efficiency of attention control, but does *not* support more specific predictions. Specifically, and contrary to ACT, our findings suggest that:

- 1) suboptimal allocation of cognitive processing resources is not dependent on

the erosion of executively-driven attention control mechanisms; and 2) anxiety did not affect top-down inhibition. These mixed results suggest a possible need to revise ACT in a way that accounts for deficits associated with non-eroded top-down control, and that better distinguishes between various types of inhibitory control.

Appendix 1. – Additional Figures

- A.1. Midline ERPs
- A.2. Full scalp ERPs – Targets
- A.3. Full scalp ERPs – Distractors
- A.4. Topographical voltage map – P3b to Targets
- A.5. Topographical voltage map – P3a to Distractors

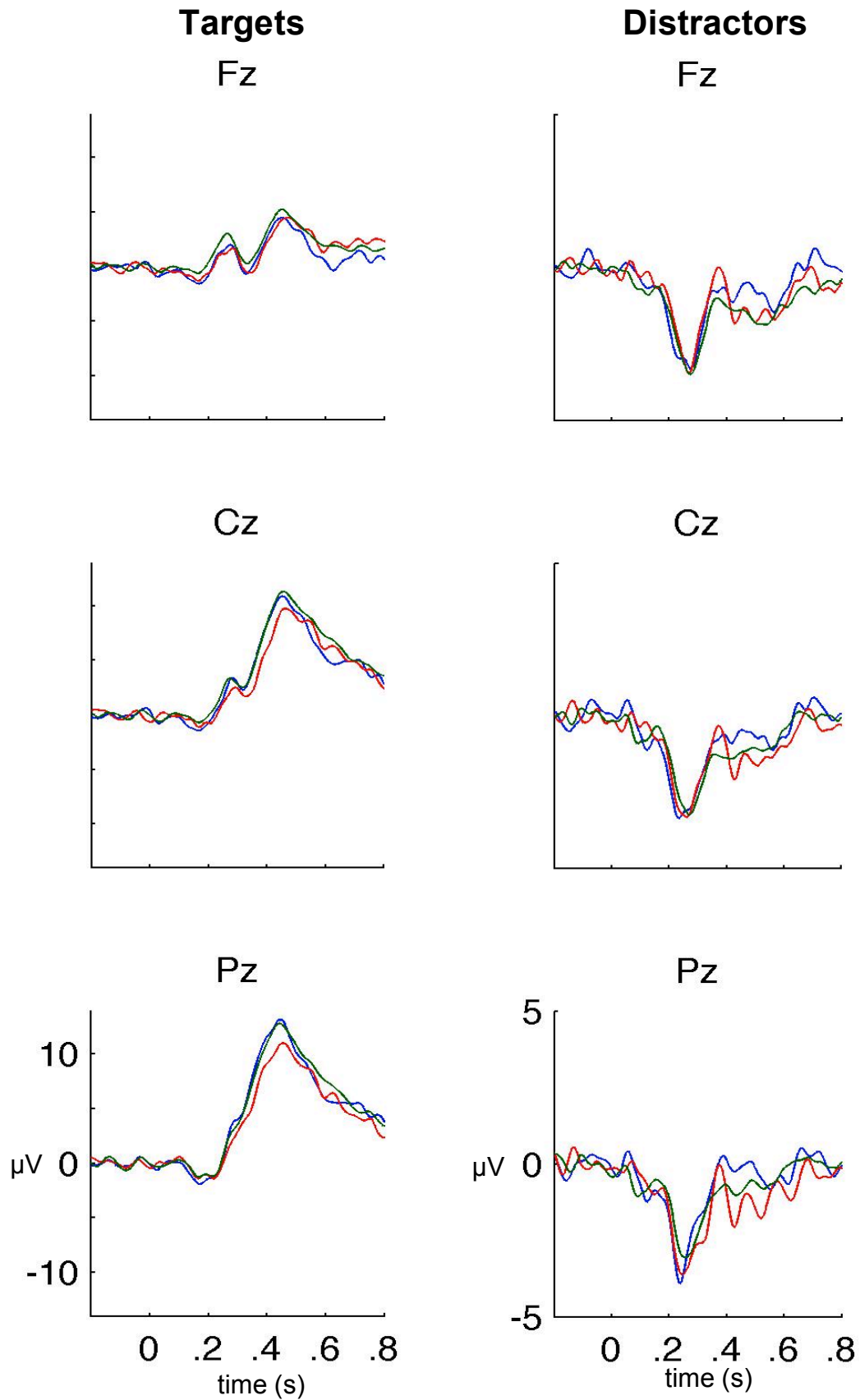
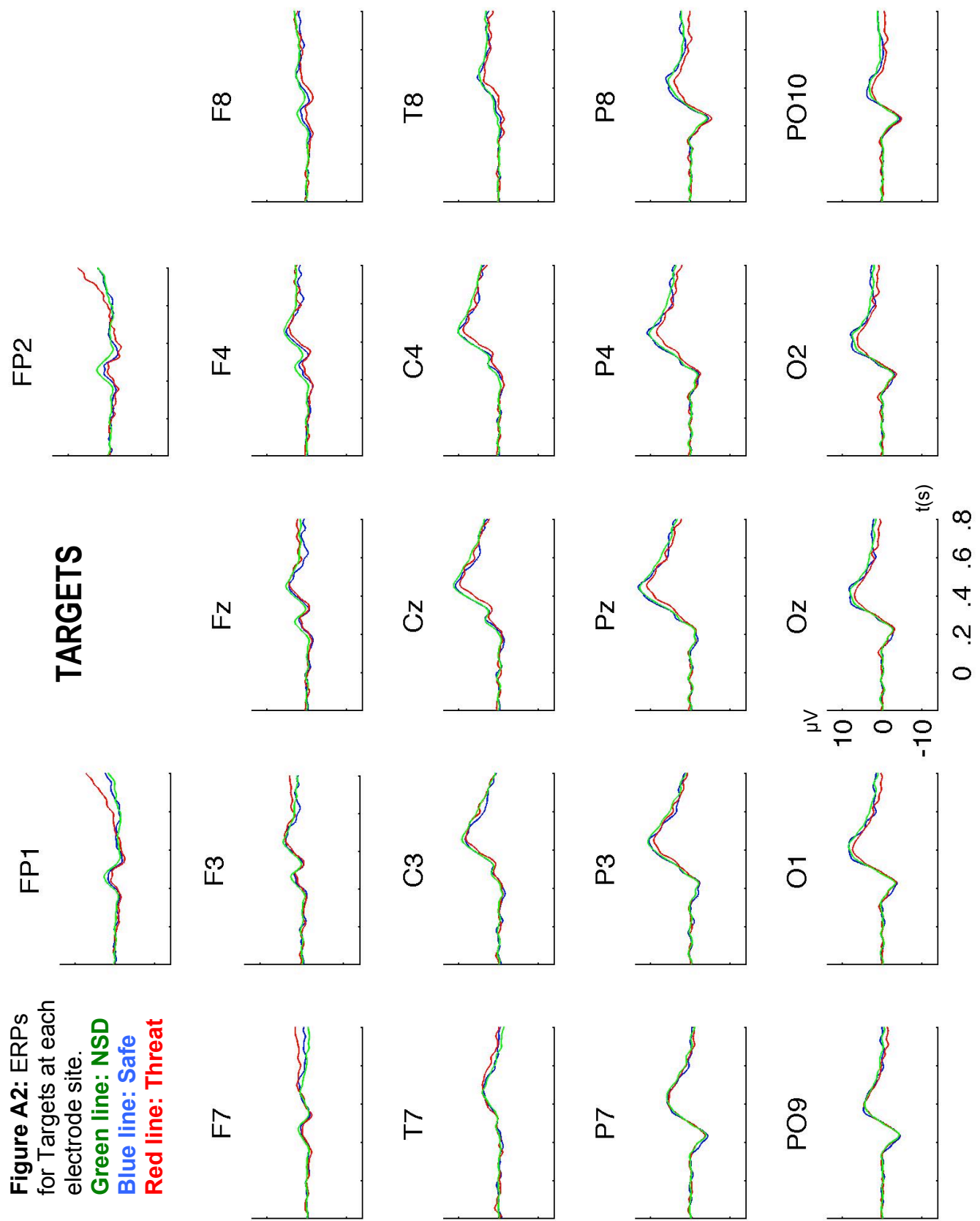


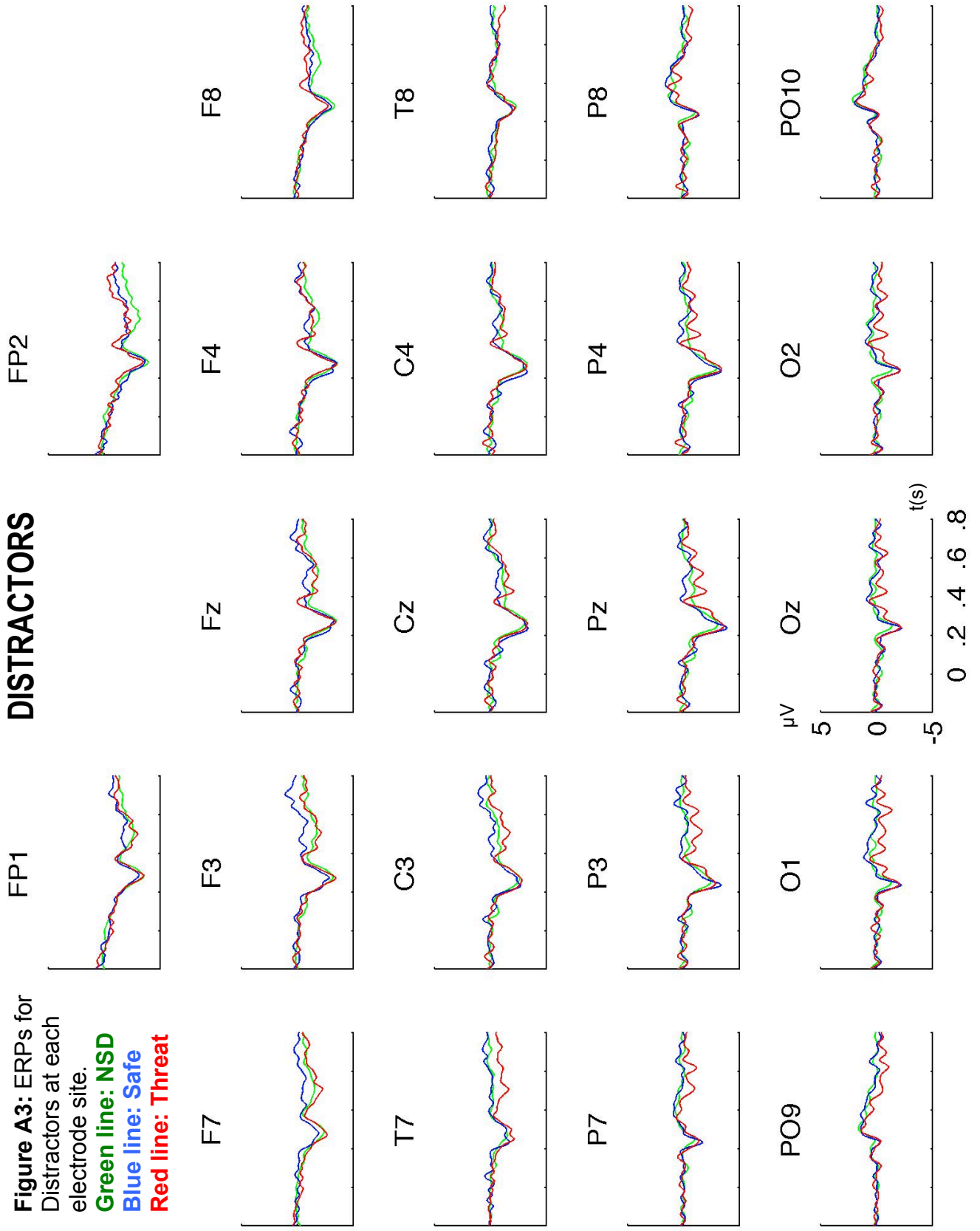
Figure A1. Midline ERPs for Targets (left) and Distractors (right).
Green line: NSD • Blue line: Safe • Red line: Threat

Figure A2: ERPs for Targets at each electrode site.
Green line: NSD
Blue line: Safe
Red line: Threat

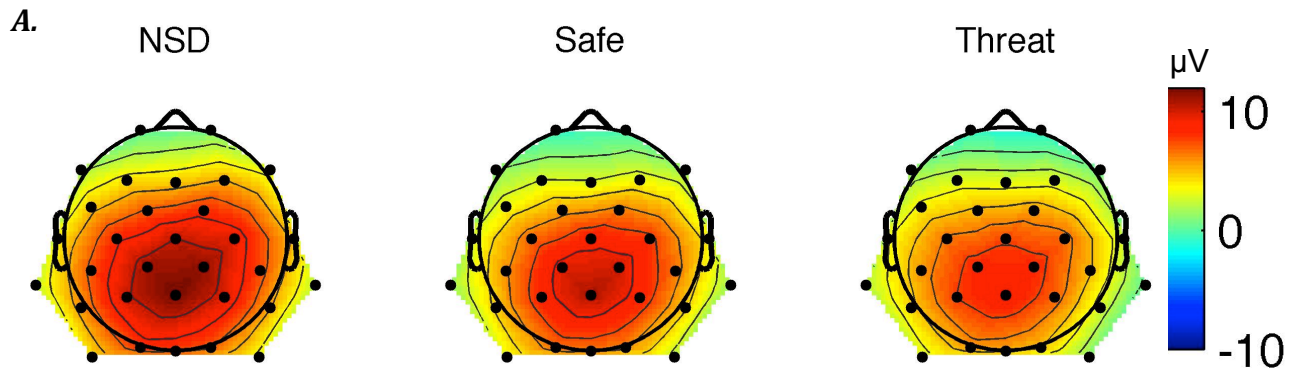


DISTRACTORS

Figure A3: ERPs for Distractors at each electrode site.
Green line: NSD
Blue line: Safe
Red line: Threat



Targets P3b



NSD-Threat

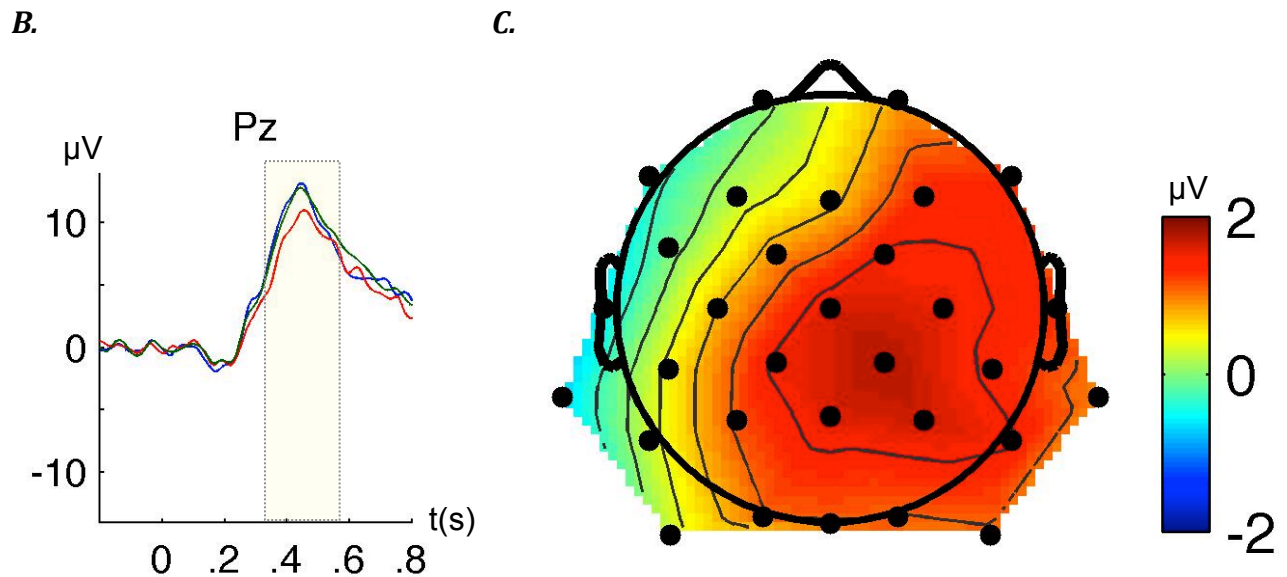
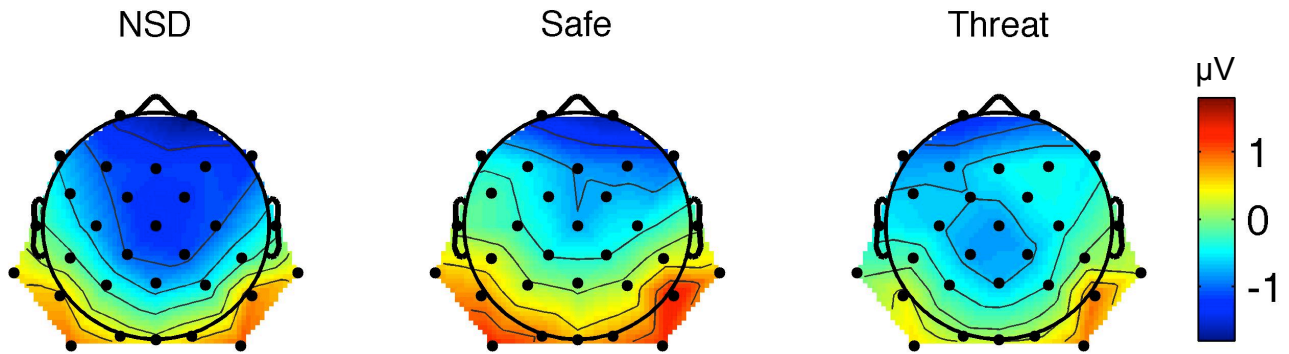


Figure A4. Topographical voltage scalp maps – P3b to Targets, 346-546ms after stimulus onset. **A.** Voltage for each condition. **B.** Voltage maps reflect average of highlighted time period in the waveform at Pz. **C.** Voltage difference between NSD and Threat conditions (NSD – Threat).

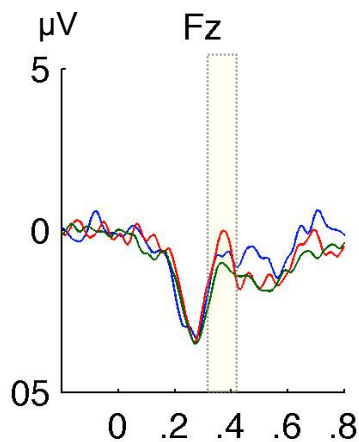
Distractors P3a

A.



NSD-Threat

B.



C.

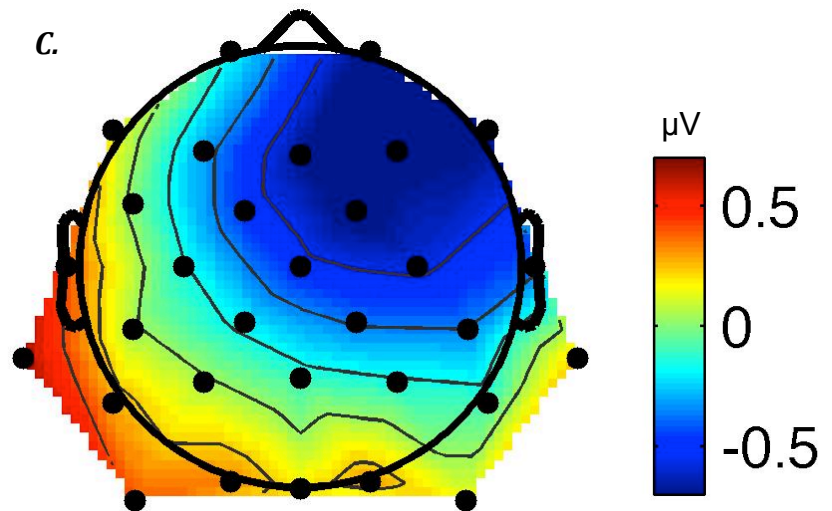


Figure A5. Topographical voltage scalp map – P3a to Distractors, 335-415ms after stimulus onset. **A.** Voltage for each condition. **B.** Voltage maps reflect average of highlighted time period in the waveform at Fz. **C.** Voltage difference between NSD and Threat conditions (NSD – Threat).

APPENDIX 2: Exploratory analysis of individual differences in ssVEP modulation

The following is a brief report of the results of an exploratory analysis of the interaction between trait anxiety and the attention-related dependent measures in Study 2.

Healthy individuals differ in their levels of Trait anxiety (STAI – Trait) and sensitivity to anxiety, and previous studies have shown those with higher Trait anxiety exhibited greater amygdala response to threatening distractors (Bishop, 2004). Since startle magnitude reflects amygdala activation we correlated difference in startle response (Threat – NoShockDay) with Trait anxiety scores. There was no relationship between the two measures ($R^2 = 0.012$, $p = .223$) but this may reflect a rather homogenous low-anxious population as opposed to a lack of relationship between startle and Trait anxiety measures.

Additionally, Trait anxiety scores correlated with N1 amplitude in an inhibitory task (Sehlmeyer et al., 2010) suggesting reaction to anxious states affected the magnitude of neural response to a rare stimulus. ssVEPs are correlated with the N1 and other early ERP components (Müller & Hillyard, 2000) so it may be that they their modulation covaries as a function of anxious predisposition. One study examining ssVEP response to angry faces only found an effect in high anxious individuals (Wieser et al., 2011). For these reasons we examined whether Trait anxiety was related to the ssVEPs measured from our sample. To do this we

split the sample in terms of their Trait anxiety scores, and entered ssVEP AMI scores into a group (2) X condition (3) ANOVA.

The omnibus test for the 8.6Hz ssVEP was significant ($F_{(2,96)} = 3.317, p = .04$) suggesting an interaction between Trait anxiety levels and 8.6Hz ssVEP modulation across conditions. There was no such interaction in the 12Hz ssVEP. Given the number of exploratory comparisons we performed, the effect would not survive the appropriate correction to control for Type I error, thus we recommend further investigation into individual differences of ssVEP modulation under anxiety that includes a sample with a broader distribution of trait anxiety and anxiety sensitivity scores.

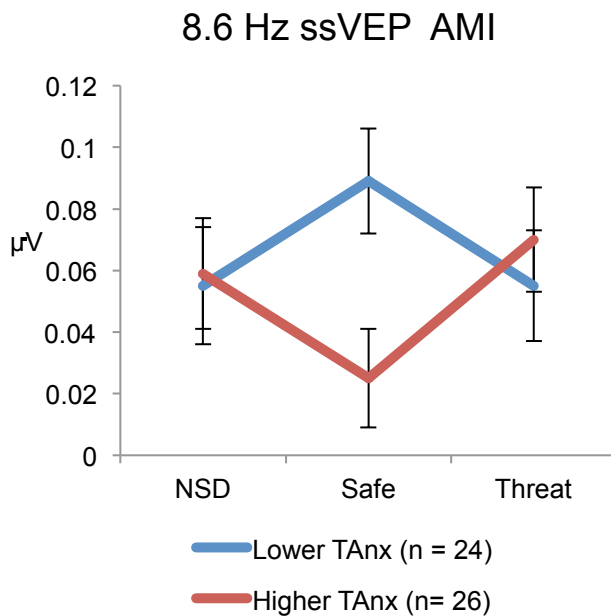


Figure A4.1. Condition x group (Trait Anxiety, median split) interaction for the 8.6Hz ssVEP. Difference between groups during the Safe condition did not survive post hoc corrections.

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