Electrical neuroimaging reveals content-specific effects of threat in primary visual cortex and fronto-parietal attentional networks

Running head:

State-dependent modulation of selective attention

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Abstract

Whereas effects of anticipatory anxiety on attention are usually assumed to remain largely undifferentiated, discrepant findings in the literature suggest that, depending on its content and causes, different modulatory effects on attention control and early sensory processing may arise. Using electrical neuroimaging and psychophysiology in a cross-over design, we tested the hypothesis that different types of anticipatory anxiety (bodily vs. psychological), transiently induced in healthy participants, had dissociable effects on brain systems regulating attention control. Attention control corresponded to the ability to maintain efficient goal-directed processing (indexed by the P300 ERP component and by activations in the attentional networks), as well as the ability to filter out irrelevant stimuli in early sensory cortex (C1 component, indexing attentional gating in V1). Results showed that while psychosocial threat, very much like perceptual load, primarily led to a stronger gating in V1, bodily threat resulted in impaired goal-directed processing within the fronto-parietal attentional network, as well as decreased filtering in V1. These results suggest that anticipatory anxiety is multifaceted, exerting different effects on attention control and early visual processing depending on its sub-type.

Keywords:

Attention, C1, ERP, fronto parietal attentional network, state anxiety

1. Introduction

Attention can bias sensory processing early on following stimulus onset. In monkeys, as well as in humans, top-down attention gating effects have been shown as early as in the thalamic nuclei (Fischer and Whitney 2012; McAlonan et al., 2008; O'Connor et al., 2002) and V1 (Schwartz et al., 2005). Yet, affective states provide powerful motivational drives that can influence attentional deployment, sometimes conflicting with top-down goal setting. Sustained anxious anticipation (Davis et al., 2010) of unpredictable and uncontrollable bodily harm (uncued delivery of electric shocks, for example) has consistently been implicated in humans and animals in hypervigilant threat monitoring (Alvarez et al., 2011; Davis and Whalen, 2001; Somerville et al., 2010), which is related to augmented sensory vigilance in order to facilitate threat detection. Critically, although anxious hypervigilance can foster an effective monitoring of the environment, it comes at a price. Stress and anxiety have been shown to induce neural plasticity in key regions such as the hippocampus, the amygdala and the prefrontal cortex (Leuner and Shors 2013; McEwen et al., 2012), altering cognitive functions, such as emotion regulation, attentional control (Arnsten 2009; Bishop 2007; Eysenck et al., 2007; Plessow et al., 2011) and goal-directed stimulus processing (Moser et al., 2005; Shackman et al., 2011).

However, outside the laboratory, threatening events are not restricted to the imminence of potential bodily harm: uncertainty, social stressors, or upsetting visual scenes are also able to trigger anxious responses, implicating activations in the extended amygdala, similarly to physical threats (Grupe et al., 2012; Yassa et al., 2012). Unlike bodily harm, these psychosocial strains have been suggested to *narrow* the attentional scope, resulting in decreased early visual responses to irrelevant sensory information (Easterbrook, 1959; Rossi and Pourtois 2012a; Schmitz et al., 2009), without systematically affecting goal-directed behavior. By comparison,

sustained anxiety related to the anticipation of uncontrollable physical harm seems mainly to impair attentional control functions, in favor of a bottom-up (ventral) attentional system, which might mediate hypervigilance (thus, *enhanced* responses to task-irrelevant, but potentially threatening information, see also Bishop et al., 2004; Choi et al., 2012; Cornwell et al., 2011; Pourtois et al., 2013).

Furthermore, negative affect can be elicited by increasing task difficulty alone, in the absence of a direct mood induction (Nummenmaa and Niemi, 2004). Hence, the typical narrowing of the attentional focus associated with high load tasks (Lavie, 2005; Rauss et al., 2009; Schwartz et al., 2005) might actually be conflated by an uncontrolled increase of negative affect, given that this state has also been related to narrowed attention (Easterbrook, 1959).

Thus, although different forms of anticipatory anxiety and distress seem to impinge on stimulus processing in dissociable ways, no study to date has directly compared their differential effects on specific attention control processes. This may be explained by the challenges posed by bringing up these different affective states in the laboratory and comparing them in a systematic way. For example, matching negative affect intensity between different types of strain (physical vs. psychosocial) appears especially challenging in between-subjects experimental designs. On the other hand, having the same participants experience these different strains in a within-subject design may lead to uncontrolled carryover, with the residual effects of one specific state possibly contaminating the subsequent one.

To overcome these problems, we used in this study a novel experimental design enabling to compare in the same participants the effects of two different types of anticipatory anxiety (physical vs. psychosocial) on the electrophysiological markers of attention control, while minimizing systematic carryover effects. In this paper, we operationalized anticipatory anxiety,

or state anxiety, as a state of sustained tension in the anticipation of the possible encounter with a negative event which is not imminent, but looming (Davis et al., 2010). We continuously measured the skin conductance levels (SCL) to monitor peripheral arousal during the experience of state anxiety, in order to be able to model the physiological response corresponding to the stressor anticipation against the normal habituation curves (measured in a condition in which no stressors were expected). Two types of anticipatory anxiety inductions (physical vs. psychosocial) were chosen given their similarity to published procedures in the literature. For each of them, we could then formulate a clear prediction regarding the specificity of its effects on attentional processes: while the threat of bodily harm would primarily impair goal-directed processing (see for example Shackman et al., 2011), by contrast, an "internal" psychological stressor should be accompanied by a narrowing of the attention focus (e.g., Rossi an Pourtois 2012a; Schmitz et al., 2009). In agreement with previous reports, we formally operationalized attention control was as the ability to maintain efficient goal-directed processing (indexed by the P300 ERP component, see Shackman et al., 2011), as well as the ability to filter out irrelevant stimuli in early sensory cortex (C1 component, indexing attentional gating in V1, see Rauss et al., 2011). We compared effects of anticipatory anxiety driven by physical vs. psychosocial threat on attention control brain processes to a third condition, consisting of enhanced perceptual load, given its well-known effects on both goal-directed processing within the fronto-parietal network (e.g., Lavie 2005; Schwartz et al., 2005) and early attentional filtering in the primary visual cortex (see Rauss et al., 2009, 2011). Importantly, by measuring self-report distress and autonomic arousal responses, we could also assess whether a possible increase in negative affect would arise in this condition (albeit of lower magnitude compared to the two state anxiety

conditions), an element which has typically been overlooked in earlier studies investigating effects of load on attention selection.

At the behavioral level, we expected high load to slow down reaction times and decrease accuracy for target detection, compared to low load. Since psychosocial threat does not seem to systematically affect overt behavior (no effects on target detection or discrimination were reported in studies investigating the narrowing of attention during negative affect induced by feedbacks or upsetting picture presentation; see Moriya and Nittono 2011; Rossi and Pourtois, 2012a and 2013; Schmitz and De Rosa, 2011), we therefore surmised that task performance would not be influenced by this form of anticipatory anxiety. Concerning the effects of bodily threat, a recent review by Robinson and colleagues (2013) highlighted the lack of consistency in behavioral costs during the anticipation of unpredictable noxious stimuli (threat of mild electric shocks). Nevertheless, two recent electrophysiological studies using the threat of bodily harm (Moser et al., 2005; Shackman et al., 2011) did not report differential effects at the behavioral level between the safe vs. threat condition. Accordingly, we reckoned that bodily threat would not lead to an impaired behavioral performance in this experiment.

However, based on existing dissociations in the literature (e.g., peripheral distractor processing seems to be either decreased or increased under stress depending on situational factors, see Choi et al., 2012 and Schmitz et al., 2009), we predicted that the two types of strains (physical vs. psychosocial) would have dissociable effects on attention control at the electrophysiological level. Hypervigilance and reduced goal-directed processing were hypothesized to be related to the threat of bodily harm, selectively (Choi et al., 2012; Moser et al., 2005; Shackman et al., 2011). Sensory hypervigilance would primarily be translated in maintained or increased early responses to irrelevant information in V1 (C1 component, Weymar et al., 2013) accompanied by

an attenuation of goal-directed processing as measured in amplitude of the target-locked P300 (Moser et al., 2005; Shackman et al., 2011). By comparison, we surmised psychosocial threat to narrow the attentional focus around fixation, and therefore selectively increase filtering of peripheral (irrelevant) information in V1 (C1 component). At the same time, goal-directed processing should remain relatively unaffected, as previously reported (Moriya and Nittono 2011; Rossi & Pourtois 2012a; Schmitz et al., 2009).

To corroborate the assumption of systematic changes in the fronto-parietal network during goal directed processing (P300 effect) as well as in V1 during the early filtering of irrelevant information (C1 effect) as a function of these two strains, we estimated the intra-cerebral sources of these two ERP components using a distributed inverse solution (standardized Low Resolution Electrical Tomography, sLORETA).

2. Materials and Methods

2.1 Participants

Twenty-six right handed undergraduates participated in the study (mean age = 20.4 years, S.D. = 2.2 years, 7 males). Participants had normal or corrected-to-normal vision, were unaware of the purpose of the study and declared no history of psychiatric or neurological disorders, nor the use of psychoactive medication. The study protocol was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee.

2.2 Stimuli and Task

The paradigm was adapted from Rossi and Pourtois (2012a). Participants monitored at fixation a rapid serial visual presentation (RSVP) of tilted gray line segments presented on a black background. Randomly intermixed with standard lines (tilted 35°), target lines with a slightly

different in-plane orientation (either 25° or 45°) were presented, with a standard/target ratio of 4/1. Participants were instructed to detect targets in the RSVP and respond with a key press. Target and standard lines were presented for 250 ms, with an average ISI of 1325 ms (range 1150-1500 ms). Peripheral, non predictive visual textures composed of horizontal line segments (8.8^{o} x 34^{o} of visual angle) were flashed for 250 ms in the upper visual field during the ISI, in 50% of the trials (see Fig. 1a). These unpredictable and uninformative peripheral stimuli were previously associated with the generation of a reliable C1 component, with its main generators source-localized in V1 (Pourtois et al., 2008; Rauss et al., 2009). In the other 50% of the trials, no peripheral stimulus was shown in periphery during the ISI, but in order to maintain the exact same temporal structure for all trials a black dummy was presented for the same duration (invisible to the participants).

The experimental session comprised a practice block (24 central stimuli, 12 followed by a peripheral irrelevant stimulus and 12 followed by the dummy), and 8 task blocks (each block comprised 100 central stimuli, 50 followed by a peripheral irrelevant stimulus). Unknown to participants, the eight blocks were equally divided into four conditions (see Fig. 1b). Each condition (Control, Load, Bodily Threat - BT, and Psychosocial Threat - PST) was composed by 2 consecutive blocks: a Baseline and a Test block. The critical manipulations were always applied during (or prior to) the Test blocks, with the Baseline blocks being identical across all four conditions.

In the Control condition, Baseline and Test block were identical (the Test block was simply the repetition of a new Baseline block), controlling for possible unspecific time or repetition effects (Grill-Spector et al., 2006).

In the Test block of the Load condition, the angular difference between standard and target stimuli was reduced to 3^{o}, thus enhancing the perceptual load of the task at fixation (High Load, HL).

In the Bodily Threat (BT) condition, participants were asked to wear EEG-compatible insert earphones (3M E-A-RTONE-3A, 10 Ohms), and were presented, before each of the two blocks, with an example of a sound. Before the Baseline block they received a low-volume, non-threatening sine wave (1000 Hz, 60 dB volume, 200 ms duration). Participants had to rate it for unpleasantness and painfulness, and were explicitly instructed that during the immediately following block they might receive, randomly interspersed in the sequence of visual stimuli, the same sound again (they all received 5 repetitions, interval: 10-35 seconds). These neutral (safe) auditory probes in the baseline block did not interfere with performance, nor did they elicit any detectable skin conductance responses. Before the Test block, participants received a white noise burst example (100 dB, 50 ms duration). Again, after rating it, the written instructions explained that they could receive the same sound again during the immediately subsequent block (5 repetitions were delivered, interval: 10-35 seconds). The onset of all sounds remained fully unpredictable (sounds were presented in between trials, not during any visual stimulus nor at their offset), and were fully unrelated to behavioral performance, as explicitly explained to participants. During the Test block, the aversive auditory stimuli were expected to reliably elicit an anxious response, usually detectable in the increased heart rate and bodily arousal (Lovallo 2005). In our study, we used tonic SCL and phasic Skin Conductance Responses (SCR) in order to corroborate the differential physiological response induced by safe and aversive sounds.

In the Psychosocial Threat (PST) condition, at the end of the baseline block an unexpected bogus feedback was presented on screen for 20 seconds. Allegedly, this feedback was informing the

participants on their performance regarding the previous block (i.e., Baseline block), providing a direct comparison with a group of matched participants. In fact, this feedback was negative for every participant, always indicating that the performance was substantially lower as compared to a group of peers. This specific procedure has previously been shown to reliably induce state anxiety, negative affect and rumination (Nummenmaa and Niemi 2004; Zoccola et al., 2012; Rossi and Pourtois 2012a, 2013). In particular Nummenmaa and Niemi (2004) clearly showed in a meta-analysis that social comparative feedback informing about success-failure (i.e., self-efficacy) provide a more ecologically valid and reliable manipulation to elicit negative affect and a transient state of anxiety, sadness or depression, than mere picture presentation or imagination. In our paradigm, a written message and a pseudo-randomly generated scatterplot were used to convey the negative evaluation. Right after this feedback, participants were instructed that they would receive a new evaluation after the following block (Test block of the PST condition), and that the next feedback would also be visible to the experimenter outside the faraday cabin, in order to maximize the likelihood of generating a sustained emotional anticipatory reaction (carrying an anxious component). Note that these specific parameters were used because they were tested and validated earlier (see Rossi and Pourtois, 2012a, 2013), and clear predictions could therefore be formulated regarding their actual impact on the amplitude of the ERP components of interest in this experiment (i.e., lower C1 to peripheral distractor stimuli but unchanged P300 to central target stimuli).

2.3 Procedure

Participants were required to sign an informed consent form, completed the first self-report measure of state anxiety (Spielberger 1983) and were then prepared for the EEG recording. During the task they sat in a dimly lit cabin, at 57 cm from a 19'' CRT screen, with head motions

restrained by a chinrest. Initially, they received detailed instructions on the detection task, then completed the practice block and the four pairs of task blocks (Control, Load, BT and PST conditions). Participants were never informed about the differences across conditions, or between Baseline and Test blocks. However, they were told that task difficulty might vary across successive blocks, at any moment during the session. This set-up enabled us to apply within-subject comparisons of attentional and affective states effects, in a cross-over design. Using this procedure, each manipulation had therefore its respective baseline block, used as reference for the statistical analyses, in such a way to control for undesired repetition or habituation effects. The order of the four pairs of blocks was counterbalanced across participants, with the exception that the PST condition was always administered last, to avoid carryover effects of the aversive feedback on subsequent blocks.

We repeatedly measured levels of anxiety and distress during the experimental session. More specifically, participants were asked to report, using two horizontal, digital Visual Analog Scales (VASes, *pleasantness* and *tension*), their subjective affective state after each block (eight times in total). Because of these multiple measurements occurring within a short period of time (roughly every three minutes), we explicitly chose for VASes, as opposed to other instruments (the STAI-S for example). VASes are generally easy and intuitive to fill out by the participants and they are actually better (more sensitive) than lengthy inventories to capture mild and fast-evolving changes in levels of state anxiety (Rossi and Pourtois 2012b).

At the end of the experimental session participants completed two more blocks (passive viewing conditions) that were used as an independent localizer for the C1 component generated in response to the peripheral texture stimuli (see Rossi and Pourtois 2012a; Vanlessen et al., 2013, in press, for similar procedures). Data for the localizer block for two participants were not

recorded due to system failure. Therefore, comparisons across task and localizer were performed on the 24 participants for which the dataset was complete.

Finally, participants filled out a second State Anxiety Inventory (STAI-S) and additional trait-related questionnaires: STAI-T (Spielberger 1983); BIS/BAS (Carver and White 1994); RRS, Ruminative Response Scale (Nolen-Hoeksema and Morrow 1991) before leaving the experimental room and receiving a complete debriefing about the goal of the study.

2.4 Electrophysiological data recording

EEG was continuously recorded from 128 active Ag/AgCl electrodes evenly distributed over the scalp surface using an elastic cap (Biosemi Active Two System, http://www.biosemi.com), following the ABC layout. Signals were referenced online to the CMS–DRL ground (driving the average potential across the montage as close as possible to the amplifier zero), and digitized at 512 Hz. CMS and DRL electrodes were embedded in the elastic cap at equidistant positions left and right of CPz. DC offsets were kept within a ±20 mV range. Vertical and horizontal oculograms were monitored through bipolar electrodes positioned on the outer canthus of each eye and above and below the left eye. Two additional sensors for off-line referencing were placed on the mastoid bones.

Two bipolar electrodes were also applied to the volar surfaces of the medial phalanges of the left hand in order to record the galvanic skin response throughout the experimental session. Participants were instructed to comfortably lay their left forearm on the table and asked not to move during the experimental blocks.

2.5 Data reduction and Analysis

Reaction Times (RTs) for correct target detections and accuracy scores (proportion of hits and correct rejections over the total amount of trials) were computed separately for each block and condition.

Changes in affective state were tested by analyzing the self-report scores obtained after each block. The scores for the two VASs were combined in one compound score, with the pleasantness VAS reverse-scored (Rossi and Pourtois 2012b). Therefore, higher scores indicate higher anticipatory anxiety and distress.

Behavioral measures (RTs, Accuracy) and self-report affect scores were analyzed with repeated measures analyses of variance (ANOVAs) with Condition (4 levels: Control, Load, BT, PST) and Block (2 levels: Baseline, Test) as within-subject factors. Significant interaction effects were followed up by univariate ANOVAs, separately per condition, with Block as Factor.

In order to compare levels of peripheral arousal during the different conditions, the continuously recorded SCL signals were segmented based on the onset of each of the eight experimental blocks, in epochs of 143 seconds (block duration). The average SCL values in these windows were extracted and analyzed exactly as the self-report scores. Specifically for the BT condition, additional analyses were performed on the psychophysiological data. First, in order to exclude the phasic startle responses to the sounds from the evaluation of tonic arousal levels, we also measured SCL selectively in the interval preceding the delivery of each unpredictable sound ("pre-sound SCL", average of 2 seconds, 5 safe sounds in the Baseline Block, 5 aversive sounds in the Test block). The interval of 2 seconds preceding the sounds was chosen because even with the shortest possible inter-sound interval (10 seconds) the last 2 seconds fall after the interval typically used for SCR analyses (8 seconds). This measure, therefore, gives a more conservative indication of the tonic arousal level over time for the two blocks of this condition (BT), free of

the influence of phasic (SCR) responses to the aversive sounds that might have artificially enhanced the SCL levels at Test. Last, in order to gain better insight into the time course of the BT anxiety induction (explore the habituation pattern of the SCR to the repetition of the aversive sound), we also measured SCRs for each and every sound in the Baseline block (safe sounds) and compared them to the Test block (aversive sounds). SCR was quantified as the highest peak in the SCL during the 8 seconds following each sound, minus the pre-sound scores (base-to-peak scoring). Scores for the "pre-sound" SCL and for the base-to-peak SCR were submitted to separate two-ways repeated measures ANOVAs, with Block (2 levels: Baseline and Test) and Sound (5 levels, corresponding to the 5 repetitions) as factors. This way, we could thus analyze both "pure" tonic arousal (using the "pre-sound" SCL) and "pure" SCR (using the base-to peak scores following sound delivery) and therefore ascertain that the repetition of the aversive sound was accompanied by a sustained fear response.

ERP waveforms obtained from the eight task blocks were computed separately, using Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany). The continuous EEG signals were referenced offline to the linked mastoids and band-pass filtered (Butterworth 0 phase filters) between 0.016 (time constant 9.95 s, 12 dB/octave) and 70 Hz (12 dB/octave); a notch-filter (50 Hz) was additionally applied. EEG signals were then segmented relative to the onset of the visual stimuli (standards, targets and peripheral textures separately), using a 100 ms pre-stimulus interval and a 750 ms post-stimulus interval. In order to avoid possible contamination from target processing and response movements on the perceptual processing of the peripheral stimuli, only textures following correctly identified *standard* stimuli (thus, not requiring a motor response) were included in the averages. Eye-blink artifacts were detected and corrected (Gratton et al., 1983). Individual epochs were baseline-corrected using the entire pre-stimulus interval,

and all epochs affected by residual artifacts were semi-automatically rejected on the basis of an absolute voltage criterion (± 75 μV relative to baseline, average rejected trials 13.1%). Individual ERP averages for central targets and peripheral irrelevant stimuli were computed as a function of Condition and Block, before grand-average waveforms were calculated.

For the independent localizer blocks, ERPs in response to the peripheral textures presented either below or above fixation were analyzed and averaged separately, following the same procedure and using the same parameters as for the peripheral textures presented during the task. Results showed a clear polarity reversal for stimuli presented in the upper vs. lower visual field, with a distribution of the component at parieto-occipital leads (peak: 75 ms for UVF; 74 ms for LVF).

We first used the independent localizer to ascertain that the C1 component in response to the peripheral stimuli had a similar topographical distribution across all task conditions, and that this distribution did not differ from the localizer block, where no central stimuli were presented. We tested this hypothesis using reference-free topographical ERP mapping analyses (performed using CARTOOL software 3.43: http://brainmapping.unige.ch/Cartool.htm). To this end, the dominant microstates (topographical maps) for a large time window encompassing the C1 and P1 components (0-150 ms after peripheral stimulus onset) were identified in the grand averaged ERP data (8 task conditions and localizer together) by means of a standard K-Means spatiotemporal clustering algorithm. A cross-validation criterion was used to identify the optimal number of dominant maps accounting for the variance in these ERP data (Pascual-Marqui et al., 1995). The dominant topographical map corresponding to the C1 component (given its latency, polarity and geometry) was then fitted back to the individual subjects data such as to extract its Global Explained Variance (GEV) or goodness of fit, in an interval in which the map was present for all conditions and blocks (49-100 ms). Statistical analyses on the GEV of this

dominant map confirmed the assumption that the C1 map explained comparable variance across task blocks and localizer (all $T_{23} < 1.04$, all p = n.s). Based on the results obtained from this data-driven topographical analysis, as well as on previous literature (Fu et al., 2012; Rauss et al., 2009, 2012; Rossi and Pourtois 2012a) we then performed a classical peak analysis for the C1 component in the task blocks. The visual C1 in response to the peripheral stimuli during the eight test blocks was semi-automatically identified as the most negative peak present in the stimulus-locked ERPs between 49 and 100 ms after stimulus onset, and scored at the midline leads A4/CPPz, A19/Pz, A20/PPOz and A21/POz (independent scoring). Given that no differences in peak latency were evident across conditions in the grand-averaged data, consistent with previous studies focused on perceptual load (Rauss et al., 2009, 2012), we primarily run statistical analyses on the peak amplitude of the C1 component. Moreover, based on previous studies no reliable differences as a function of affective state were expected on later ERP components, such as the P1-midline or N1 (Rossi and Pourtois 2012a; Vanlessen et al., 2013, in press). Therefore, these additional analyses are not reported here.

To investigate goal-directed processing, we analyzed amplitude variations of the P300 component in response to correctly identified target stimuli, as a function of condition and block. Given the slow and sustained nature of the P300 in this task, in order to objectively define the temporal windows for the scalp ERP and source reconstruction analyses, we first run a topographical mapping analysis as described here above, on a long time interval (0-750 ms after central stimulus onset). The dominant P300 map, characterized by a centro-parietal positivity, was clearly identifiable and consistently present for all conditions and blocks, starting at ~430 ms (latest onset, Load Test block). Therefore, based on these topographical results and on earlier studies (Kim et al., 2008; McCarthy and Donchin 1981; Sawaki and Katayama 2007), we

analyzed the P300 with a standard mean amplitude analysis in an interval of 250 ms (430-680 ms), at centro-parietal-occipital leads (A4/CPPz, A19/Pz, A20/PPOz and A21/POz) along the midline. Using the same parameters, we also analyzed the P300 generated in response to the central standard stimuli (having a modest amplitude, much smaller than for target stimuli). This auxiliary analysis was important to assess whether state changes or attention/load influenced the processing of the central target selectively (as hypothesized), or instead the P300 for target and standard stimuli equally.

C1 peak and P300 mean amplitude scores were analyzed separately by means of repeated measures ANOVAs, with Lead (A4, A19, A20, A21), Condition (Control, Load, BT, PST) and Block (Baseline, Test) as within subjects factors. Significant interaction effects were followed up by univariate ANOVAs (Factor: Block; Baseline vs. Test) carried out separately for each Condition. A Greenhouse-Geisser correction was applied when sphericity was violated.

2.6 Source localization analyses

In order to estimate the neural sources underlying the ERP components (P300, C1) we used a standardized low-resolution tomography algorithm (sLORETA, Pascual-Marqui 2002, Sekihara et al., 2005). This algorithm makes use of a realistical volume conduction head model (3-compartment boundary element registered to the MNI152 template volume, see Fuchs et al., 2002). The lead field was interpolated for the ABC electrode coordinates used in this study based on the original lead field (created for a fixed set of 316 electrode positions from the 5% International system, Jurcak et al., 2007). The transformation matrix obtained with this interpolation was applied to the data extracted from Brain Vision Analyzer, converting electric potential differences to standardized current density in the brain (signal-to-noise ratio - SNR parameter used in this study = 10; 6239 voxels of cortical grey matter).

Statistical non-parametric comparisons were performed on log-transformed data using paired-samples T tests, directly contrasting Baseline and Test blocks for each experimental condition separately. Only one single T-Test was computed for each voxel/node in each time-window corresponding to the scalp topographical and ERP analyses (i.e., 430-680 ms for the P300 in response to targets, 60-80 ms for the C1 in response to peripheral stimuli, given the latency of its peak in the grand-averaged data at ~74 ms). In order to limit multiple testing error, to ascertain differential activity across conditions we selected specific regions of interest for the statistical comparisons (Schettino et al., 2013), related to a-priori anatomical hypotheses regarding the putative neural networks underlying either the C1 or P300 component. In detail, for the C1 component, V1 (BA 17) was predicted to be the key region involved in the generation of this early visual ERP component and in its amplitude variation as a function of our experimental manipulations (Kelly et al., 2008, 2013). Therefore, only voxels anatomically identified in BA 17 were eventually considered in the statistical analysis. Concerning the P300 modulations as a function of condition, we based our predictions on earlier studies exploring the functional neuro-anatomy underlying load-related effects (Desseilles et al., 2009; Juckel et al., 2012; Schwartz et al., 2005; Wojciulik et al., 1998). More specifically, clusters of activations corresponding to P300 amplitude variations as a function of Load were expected to take place within the fronto-parietal attentional networks (ACC, PCC, parietal areas 7/40 and Frontal Eye Fields). Accordingly, after having confirmed the involvement of these areas in the low vs. high load condition, we subsequently examined, in these same regions of interest, the contrast between baseline and test blocks for the other experimental conditions (i.e., mere repetition, BT or PST).

3. Results

3.1 Self report and SCL/SCR results

Prior to the start of the experimental session, participants' reported state anxiety levels were comparable to published norms (STAI-S_{pre} *M* = 35, SD = 7.4, range 20-52). At the end of the experimental session, state anxiety was significantly increased (STAI-S_{post} *M* = 40, SD = 8.5, range 23-54; $T_{25} = 4.51$, P = .0001).

To gain a better understanding of the dynamical changes in the participants' state anxiety levels, we tested whether our induction procedures were both successful in enhancing distress. Psychological feelings of tension and unpleasantness were captured by self-report measures at the end of each experimental block (Condition x Block interaction, $F_{3,75} = 6.11$, P = .001). Follow-up analyses confirmed that no increase in distress was reported when moving from Baseline to Test block in the Control condition, ($F_{1,25} = 0.10$, P = .92), while under Load ($F_{1,25} = 18.61$, P = .0002), BT ($F_{1,25} = 13.59$, P = .001) or PST ($F_{1,25} = 16.74$, P = .0004) participants experienced a combination of increased tension and decreased pleasantness (Table I and Inline Supplementary Table I).

Second, the successful elicitation of a sustained fear response, expected to be maximal for the BT condition, was confirmed by the analysis of the levels of peripheral arousal, as reflected by the SCL (interaction Condition x Block $F_{3,75} = 9.23$, P = .00003). As compared to the Baseline block, SCL was enhanced in the Test block during BT ($F_{1,25} = 13.39$, P = .001), was maintained during PST ($F_{1,25} = .42$, P = .52), while it significantly habituated in the Control and Load conditions (Control: $F_{1,25} = 4.40$, P = .046; Load: $F_{1,25} = 5.97$, P = .02; see Fig. 2a), suggesting that peripheral arousal responses selectively took place when the critical manipulations were applied, as predicted. Moreover, this analysis confirmed that the high Load block, although being more challenging at the cognitive level, did not elicit an autonomic reaction, hence providing a

second control condition to assess changes in visual processing following the induction of sustained fear.

Given that PST was always administered last for obvious methodological reasons (see above), this factor might potentially explain why we did not observe a significant SCL increase in this condition (note however that SCL clearly did not resemble the normal habituation pattern observed for the control and load conditions, suggesting that a lack of sensitivity could not explain these SCL results for the PST). To ascertain at the statistical level that this was not the case, we run several follow-up analyses. First, we established that the peripheral activation was similar across all four conditions at baseline ($F_{3,75} = 2.38$, $P = 0.10$). This result suggests that the pseu-dorandomization of conditions did not interfere with our SCL measurements *per se*. Importantly, as expected, the SCL was significantly different across conditions at test ($F_{3,75} = 8.80$, $P = 0.001$). In particular, follow up tests indicated that the SCL was the highest at test for the BT condition (see Fig. 2A), but the tonic arousal level was also higher at test for the PST condition as compared to both the control ($T_{25} = 2.18$, $P = .04$) and the load ($T_{25} = 2.46$, $P = .02$) conditions where threat was absent. Combined together, these result show that whereas PST was always administered last, a mild (compared to BT) but significant (compared to the two control conditions) defensive response arose, lending support to the assumption that PST was indeed associated with anticipatory anxiety.

Selectively for the BT, we also analyzed tonic SCL in short time windows preceding each unpredictable sound delivery, in order to ascertain that the significant increased arousal as measured by the tonic SCL could not be explained by the inclusion of the phasic responses to the aversive sounds in the measurement window. Results are shown in Fig. 2b. The ANOVA comparing SCL preceding safe vs. aversive sounds resulted in a main effect of Time ($F_{4,100} =$

16.44, P = .000006), due to the tendency of the SCL to habituate over time in both conditions. More importantly, a significant effect of Block ($F_{1,25}$ = 18.49, P = .0002) reflected enhanced tonic SCL in the Test block (when participants were aware that aversive sounds could unpredictably be delivered) as compared to the Baseline block, at all time points. The interaction term was not significant ($F_{1,25}$ = 2.11, P = .12), indicating that the hyperarousal for the BT condition was experienced throughout the duration of the threat block, and did not habituate (post-hoc paired t-tests performed for each time point suggested that the effect actually tended to increase towards the end of the block, as can be seen in Fig 2a).

The SCR results (Figure 2c) confirmed the elicitation of a reliable fear response in the test block of the BT condition. The ANOVA performed on the base-to-peak scores in the 8 seconds window following each sound indicated a main effect of Block ($F_{1,25}$ = 27.28, P = .00002) and Time ($F_{4,100}$ = 13.25, P = .00000001), and a significant interaction Time x Block ($F_{4,100}$ = 9.51, P = .000001). Follow-up univariate ANOVAs separately per block showed that the SCR to the safe sounds did not change over time ($F_{4,100}$ = 1.07, P = .36), while the response tended to diminish in size in the Test block ($F_{4,100}$ = 12.54, P = .00000003). Nevertheless, post-hoc paired t-test calculated per time point confirmed that the different in SCR was present for all repetitions, even for the last one (all T_{25} > 3.05, all PP < .01).

3.2 Behavioral results

Based on previous reports, we did not expect sustained fear to alter behavioral performance in this task. Speed and accuracy were very well balanced across Conditions and Blocks, and were affected solely by the Load manipulation (interaction effects Condition x Block: RTs: $F_{3,75}$ = 5.42, P = .006; Accuracy: $F_{3,75}$ = 75.77, P = 1.2E-22).

Follow-up ANOVAs confirmed that RTs for correct target detections were slower and accuracy was lower in the Test block of the Load condition, as compared to the reference Baseline block (RTs: $F_{1,25} = 10.51$, P = .003; Accuracy: $F_{1,25} = 122.30$, P = 4.1E-11), confirming that the perceptual Load manipulation was efficient. In all the other experimental conditions behavioral performance was unaffected by the manipulation, so that RTs and accuracy were not different between Baseline and Test blocks (all $F_{1,25} < 2.44$, all P > .13, for details see Table I). This pattern of results confirmed that anticipation anxiety for BT or PST did not influence behavioral performance.

3.3 ERP results: goal-directed stimulus processing (P300)

After the exclusion of trials in which the target was not recognized as such (Omission Errors), 75% of the trials were classified artifact free. Due to an increase of movement artifacts (startles) in the BT Test Block, the percentage of trials excluded from the analyses turned out to be different across conditions and blocks (Condition x Block interaction F3,75 = 6.48, p < .002). However, the percentage of rejected trials was higher at Test, as compared to Baseline, in the BT condition exclusively (28% vs. 14%, $T_{25} = 3.99$, P = .001). Despite this slightly different SNR between BT and the three other conditions, the topographical analysis on the target ERP responses revealed a stable solution comprising 6 different dominant topographical maps explaining 96.0% of the variance in the ERP data. This analysis clearly identified a main dominant topographical map characterized by a monopolar centro-parietal positivity (see Fig. 3a) during the time interval encompassing the P300. Given the later onset of this map in the Load condition (see Fig. 3a, load panel) we restricted all our analyses to a time interval in which the map was reliably present in all conditions (430-680 ms). As it is evident from Figure 3 (panel B),

this window encompassed the peaking interval in all conditions and blocks, thereby confirming the reliability of the results obtained with the data-driven topographical analysis.

The ANOVA on the mean amplitude data revealed a significant Condition x Block interaction ($F_{3,75} = 6.78$, $P = 0.001$). Whereas the target-related P300 component had the same magnitude between Baseline and Test blocks for the Control and the PST conditions ($F_{1,25} = 1.93$, $P = .18$ and $F_{1,25} = 0.06$, $P = .81$, respectively), it was significantly decreased when the task was performed under a higher perceptual Load ($F_{1,25} = 21.15$, $P = .0001$), but also when a sustained state of fear for BT was endured ($F_{1,25} = 10.0$, $P = .004$, see Fig. 3b and Table II).

Source localization. As predicted based on the topographical analysis, the paired comparison between Baseline and Test blocks in the perceptual Load condition revealed widespread significant clusters in areas previously associated with perceptual Load effects (see Fig. 3c, Load panel). A first cluster was localized in the Posterior Cingulate Cortex [PCC, Brodmann's Area (BA) 23, Talairach coordinates at max: 5*x*; -33*y*; 25*z*; $T_{25} = 3.59$, $P = .001$]. This same cluster, although reduced in size, showed reduced activation under BT (PCC, BA 23, Talairach coordinates at max: -5*x*; -38*y*; 25*z*; $T_{25} = 2.72$, $P = .01$, Fig. 3c, BT panel). By comparison, no suprathreshold node was evidenced in this area for the Control condition (all $T_{25} < |1.75|$, all $P > .09$) or the PST (all $T_{25} < |1.49|$, all $P > .15$), when comparing Baseline to Test blocks. A second non-overlapping cluster was, conversely, more active during the high perceptual Load block (test > baseline block), encompassing cortical areas classically involved in the voluntary control of attention in high load situations. It comprised a portion of the medial wall of the (pre)frontal cortex, including the Anterior Cingulate Cortex (ACC, BA 32, Talairach coordinates at max: -55*x*; 43*y*; -6*z*; $T_{25} = -2.35$, $P = .03$). This cluster extended dorsally, and encompassed the Frontal Eye Fields (BA 8, Talairach coordinates at max: 35*x*; 31*y*; 44*z*; $T_{25} = -4.07$, $P = .0004$), while

more caudally, it included a large portion of the parietal lobes, bilaterally (BA7/40, Talairach coordinates at max: -54*x*; -23*y*; 29*z*; T_{25} = -5.39, P = .00001).

Crucially, while both the prefrontal (BA 8 Talairach coordinates at max: -25*x*; 22*y*; 50*z*; T_{25} = -3.42, P = .002) and the parietal areas (BA7/40, Talairach coordinates at max: 10*x*; -75*y*; 50*z*; T_{25} = -3.20, P = .004) were also more active after the manipulation than at baseline in the BT condition, activity in the ACC was not significantly increased.

Interestingly, in the PST condition part of the ACC was also more strongly activated in the Test as compared to the Baseline block, (BA 32, Talairach coordinates at max: 10*x*; 26*y*; 26*z*; T_{25} = -2.73, P = .01). However, this effect did not overlap with the ROI involved in the load manipulation: it included neither the FEF, nor the parietal region (all $T_{25} < |1.92|$, P > .06), but it extended along the median surface of the frontal lobe and encompassed BA 24 (max T_{25} = -2.75, P = .01, see Fig 3c, PST panel).

Finally, in the Control condition, the source localization analysis did not reveal any increased recruitment of ACC or dorsal fronto-parietal attentional network, but on the contrary, even a reduced activity for the test relative to the baseline block in the posterior parietal region (T_{25} = 3.28, P = .003), suggesting that repetition alone could not explain the results found for either Load, BT or PST.

3.4 ERP results: control analysis on late processing of standard stimuli

An average of 78% artifact-free trials were included in the analyses (this percentage was comparable across conditions and blocks: all $F3,75 < 2.66$, all p > .08). As expected, the standard stimuli did not elicit any clear P300 (see Inline Supplementary Figure 1). However, we also analyzed the amplitude of the ERP response to these standard stimuli in the same window used to extract the target P300 component (see above). This analysis showed a significant Condition

x Block interaction ($F_{3,75}$ = 4.83, P = 0.004), which was explained by a change of the ERP amplitude in the Control condition, selectively. In this condition the ERP amplitude for standard stimuli was further reduced in the Test as compared to the Baseline block (M_{base} = 2.97 μV; M_{test} = 1.42 μV; $F_{1,25}$ = 11.41, P = .002). In all the other conditions, the standard stimuli elicited similar (and very modest) ERP activities during this interval in baseline vs. test blocks (Load: $F_{1,25}$ = 0.17, P = .68; BT: $F_{1,25}$ = 2.67, P = .12; PST: $F_{1,25}$ = 3.16, P = .09).

3.5 ERP results: early gating in visual cortex (C1)

An average of 75% of artifact-free trials were included in the analyses, and this percentage was comparable across conditions and blocks: all F3,75 < 2.16, all p > .12). The topographical analysis revealed a stable solution with 4 dominant maps explaining 94.4% of the variance of the C1-P1 ERP data (two maps in the P1 interval were correlated for 97%, and were therefore merged, resulting in a solution with 3 dominant maps). A separate solution with 4 4 maps (explaining 96.7% of the variance) was obtained for the stimuli showed in the lower visual field (only localizer block, see Fig. 4a). A dominant topographical map characterized by a parieto-occipital negativity along the midline was evidenced during the C1 interval for both task blocks and localizer block, when stimuli where presented in the upper visual field (49-100 ms following stimulus onset, see Fig. 4a).

Once ascertained that the topographical distribution of the C1 component was comparable across conditions, we performed a peak amplitude analysis (Fig. 4b), at the scalp leads where this component was maximally expressed (occipito-parietal midline leads). As predicted, the critical interaction Condition x Block was significant ($F_{3,75}$ = 3.07, P = 0.03). Follow up analyses on the Control condition evidenced no change of the C1 amplitude for the test, relative to the baseline block ($F_{1,25}$ = 0.25, P = .62), while during Load ($F_{1,25}$ = 9.60, P = .005) and anticipatory anxiety

of PST ($F_{1,25}$ = 17.52, P = .0003) a lower C1 amplitude was recorded during the Test block, compared to the respective Baseline block (Fig. 5a). No significant amplitude change of the C1 was evidenced in the BT condition ($F_{1,25}$ = 0.11, P = .74). To put to the test one of our main predictions, the critical difference (Baseline - Test) for the amplitude of the C1 was directly compared between the two types of sustained fear. We reasoned that if PST was sufficient to cause an early narrowing of the attentional scope, whereas the monitoring for BT was expected to loosen attentional control and augment sensory vigilance, then the direct contrast between these two different affective state conditions should be significant. This auxiliary analysis confirmed this conjecture (T_{25} = 2.57, P = .016).

Source localization. The amplitude of the C1 recorded over parieto-occipital leads along the midline in response to the irrelevant peripheral stimuli was substantially reduced in the PST condition, as well as in the Load condition, to a lesser degree (see Fig. 5a). To substantiate the selective involvement of the primary visual cortex in this effect, we compared, in the inverse solution space, baseline to test blocks using paired t-tests, separately for the four experimental conditions (Fig. 5b). Results of these analyses confirmed that a cluster comprising 23 adjacent nodes localized in BA 17 was significantly less active in the Test compared to the respective Baseline block in the PST condition (BA 17, Talairach coordinates at max: 20*x*; -72*y*; 13*z*; T_{25} 3.07, P = .005). In the test block of the Load condition, we also observed a significant amplitude reduction at test of a smaller cluster of nodes in BA 17 (Talairach coordinates at max: 20*x*; -93*y*; -8*z*; T_{25} = 2.24, P = .034). No suprathreshold nodes were observed in BA 17 in the BT condition (all $T_{25} < |0.76|$, all P > .45), nor in the Control condition (all $T_{25} < |1.86|$, all P > .07).

3.6 Additional analyses controlling for arousal intensity

Although PST and BT led to similar increases in distress when this was measured using self-reports, BT was associated with a higher increase in peripheral arousal than PST (PST being in itself higher at test than the two control conditions). This element might potentially complicate the direct comparison between the effects of these two strains, given that arousal intensity is a key factor influencing attention control brain processes (for a recent review implying a direct role of the noradrenergic system in the interplay between arousal and attention control, see Sara and Bouret 2012). However, several additional control analyses allowed us to establish that the reported ERP dissociations (when contrasting BT to PST; see C1 and P3) could not easily be explained by an asymmetric level of autonomic arousal between these two conditions

If these differential ERP effects between BT and PST were merely related to the difference in intensity of physiological response, then controlling for this factor should flatten or obscure these dissociations. To test for this possibility, we first split our sample based on the peripheral arousal increase in PST (median split based on SCL delta scores, N= 13 in each group) and compared the ERP results found in these two groups. If the arousal response is a key factor influencing the effects of PST on attention control, the group showing higher arousal increases should show a strong C1 effect (and perhaps even an attenuated P300). By comparison, the group responding only mildly in terms of arousal should show smaller or null effects, both for the C1 and P300 components. On the other hand, if effects of PST on attention control are truly related to the content of this specific anticipatory anxiety manipulation (rather than the intensity of the arousal response in general), then the effects of PST on the C1 (and P300) should be similar in these two groups. A between subjects t-test confirmed that the two groups differed significantly in the intensity of their arousal response to the PST ($T_{24} = 5.52$, $P = .00001$). Critically, the paired t-tests (baseline vs. test) confirmed a large reduction of the amplitude of the C1 in both groups (T_{12}

= -2.92, P = .01, Cohen's *d* = .81;T_{12} = -2.89, P = .01, Cohen's *d* = .80, for the high and lower responders respectively), and similar non-significant changes of the P300 (T_{12} = 0.36, P = .73, Cohen's *d* = 0.10; T_{12} = 0.42, P = .68, Cohen's *d* = 0.12 for the high and low responders respectively). Next, the same median-split logic was applied to the BT condition, creating two groups that differed substantially in SCL delta scores (T_{24} = 6.58, P = .00001). In none of the two groups the C1 amplitude was influenced by this threat manipulation (T_{12} = -0.91, P = .38, Cohen's *d* = 0.25; T_{12} = 1.03, P = .33, Cohen's *d* = 0.28 for the high and low responders respectively). In this condition (BT), the intensity of the arousal response did play a role, but for the P300 component selectively. The high responder group showed a large P300 reduction (T_{12} = 3.06, P = .01, Cohen's *d* = .85), while the low responder group only showed a non-significant trend for this P300 effect (T_{12} = 1.60, P = .14, Cohen's *d* = .44).

4. Discussion

A wide range of contexts perceived as challenging, uncertain or dangerous have the potential to elicit anticipatory anxiety responses, entailing long-lasting activations in the extended amygdala (Davis and Whalen 2001; Somerville et al., 2010), and increased autonomic arousal. However, the question arises as to whether different threat-inducing situations, although sharing some common neurobiological mechanisms, actually map onto the same realm or, instead, correspond to different situations, with dissociable effects regarding attention control. In this study, we addressed this question using a cross-over experimental design, wherein effects of different types of anticipatory anxiety on visual selective attention were systematically compared at the behavioral, psychophysiological, and neural levels. Our new results endorse the idea that anticipatory anxiety is not a monolithic construct, but rather that specific dissociations arise

during attention control and early sensory processing, depending on specific affective state characteristics. These dissociations are summarized in Table II.

In the perceptual load condition, used as a second control condition, target detection was objectively more difficult, as reflected at the ERP level by a strongly reduced target P300. These late-processing modulations were estimated, in line with previous observations, in areas lying within the fronto-parietal attentional network (Corbetta and Shulman, 2002), such as the ACC and PCC, the middle and superior frontal gyri and the parietal lobe (Juckel et al., 2012; Schwartz et al., 2005; Wojciulik et al., 1998). Influential accounts of selective attention predict that conditions of high load are not only related to increased effort, but also result in diminished attentional spillover to irrelevant information (Lavie 2005). In line with this account, together with a general enhanced recruitment of attentional control areas to carry out goal-directed processing, under load we also observed increased filtering of irrelevant information in early visual pathways. The C1 elicited in response to the exact same irrelevant stimuli presented in the peripheral visual field was significantly reduced in magnitude when the task became more taxing, consistently with previous evidence (Rauss et al 2009, Rossi and Pourtois 2012a, Schwartz et al., 2005; but see Fu et al., 2012). Interestingly, we also found that negative affect was substantially increased during high compared to low load at the subjective level, in the absence of any threat induction. Accordingly, the increased filtering of peripheral information reported in this condition (C1 effect) might stem, at least partly, from this change in negative affect (as opposed to an increase in task demands alone or exclusively).

Similarly, PST, where task load was kept constant, was also associated with an enhanced level of negative affect at the subjective level (but only a mild change of SCL at the autonomic level) as well as a reduced C1 component. Noteworthy, as previously suggested (for example by Schmitz

et al., 2009), this attentional bottleneck effect did not arise at late, post-perceptual levels during stimulus processing, but as early as 75 ms following stimulus onset, hence during the earliest sweep of processing in V1, as corroborated by our source localization results. At first sight, thus, the effect of psychosocial anxiety induction on the early filtering of irrelevant information seems to mimic an enhancement of perceptual load. These changes in attention allocation captured by the C1 component are therefore not simply related to changes in bodily arousal (given that SCL remained indistinguishable from the control condition during load but was slightly enhanced during PST). On the other hand, although load and PST might share a similar attention narrowing process, these two states largely differ regarding resources allocation and the processing of the central stimuli. While load clearly dampened the amplitude of the P300 component (due to the fact that during high load the target stimuli were objectively more difficult to discriminate than during the low load), by contrast, no such effect was evidenced during the experience of psychological distress caused by social evaluation (Moriya and Nittono 2011; Rossi and Pourtois 2012a). During PST, we failed to observe systematic changes in PCC as well as frontal and parietal structures. Although under PST the estimated activation was increased in an ACC cluster, which could be taken as an indirect indication of enhanced attention control (Crottaz-Herbette and Menon, 2006), this ACC activation did not overlap with the ACC cluster observed during load, but spread dorsally in the medial frontal wall (see Fig. 3c), in areas that have previously been associated with emotion regulation (Kalisch et al., 2006). Therefore, we can tentatively argue that changes in attention control in PST might actually stem from the (spontaneous) activation of compensatory mechanisms in the medial (pre)frontal cortex (mPFC), probably meant to down-regulate the negative emotion transiently experienced. To corroborate this idea, although indirectly, we explored whether significant relationships between self-report

scores in trait rumination proneness (RRS total and brooding scores; see Nolen-Hoeksema and Morrow, 1991) and measures of state anxiety and distress during PST could be found. While at the subjective level, we only found a numerical trend towards a positive correlation between RRS Brooding and the increase in self-report tension (r = .30, P = .13 with the test-Baseline Delta score in the Tension VAS), at the physiological level significant positive linear relationships were evidenced between rumination and increase in SCL when moving from baseline to test block (r = .50, P = .009 with the Total RRS score *;* r = .44, P = .02 with the Brooding subscale). These significant correlation results suggest that participants who were prone to respond to real life stressors with ruminative and brooding thinking styles were also the ones who most strongly reacted at the autonomic level during PST. More generally, these findings thereby confirm that the PST manipulation was valid and efficient to elicit a genuine negative emotional response, which interfered with the maintenance of the current task goal and led to a narrowing of the attention focus (as captured by the C1 component). This conjecture, requiring additional empirical validation, is in line with recent findings showing that lesions in the mPFC impair appraisal of socially stressful situations, resulting in increased self-report and physiological markers of the stress response in a social stress challenge (Buchanan et al., 2010). Presumably, this compensatory mechanism might also account for the strong attentional narrowing effect observed in this condition (see C1 results), which therefore would not correspond to a voluntary phenomenon, nor a direct effect of anxiety *per se*, but instead would translate a byproduct of the competition for limited resources. Nonetheless, because the anxiety induction is ostensibly related to task performance during PST, an alternative explanation accounting for the increased activation in the ACC cluster is the anticipation of a possible repetition of the negative comparative evaluation and hence an increase in task involvement

during the test block. However, this interpretation seems at odds with the absence of behavioral effects or detectable changes in the ERP responses to either standard or target stimuli during PST. Given that this type of induction has been used and validated before in a study with multiple load levels, and neither performance nor ERP responses to central stimuli were influenced by it (Rossi and Pourtois, 2012a), an increase in attention control during PST driven by changes in motivation exclusively can be ruled out, though indirectly. Accordingly, future studies are needed to clarify whether an increase ACC activity during PST reflects enhanced attention control, a change in task involvement or alternatively specific emotion regulation processes.

During BT, in line with previous studies using anticipation of physical stressors (Moser et al., 2005; Shackman et al., 2011), target detection was preserved at the behavioral level. Nevertheless, our ERP results clearly confirm that this type of threat triggered substantial changes in brain networks responsible for goal-directed stimulus processing. Similar to Load, BT led to a clear dampening of the P300 component, with traceable effects within the PCC and fronto-parietal areas, indicating attenuated target processing. However, the recruitment of the ACC and mPFC was not increased, suggesting that this state manipulation was less pervasive than, or at least qualitatively different from, an increase in objective task difficulty. This pattern of neural activations (decreased PCC activation, and unaltered ACC/mPFC recruitment) might not only explain the drop in goal-directed stimulus processing (attenuated P300), but also potentially account for a facilitated spillover of attention to the peripheral visual field, where task-irrelevant stimuli were presented occasionally. As we show for the first time with our new results, under BT, unattended, neutral (but potentially distracting) visual information elicits a strong early response in visual areas, interpreted as an indication of inefficient filtering. These

novel findings dovetail the notion that a state in which the encounter of physical harm is expected "automatically" interferes with endogenous attentional control. Given the intrinsic motivational relevance of the threat stimuli, bottom-up characteristics such as abrupt onset might become prioritized as compared to goal-directed ones (such as targetness). Hence, any stimulus, albeit task-irrelevant, sharing these characteristics (physical saliency, abrupt onset etc.) might gain advantage in the competition for attention allocation. Altogether, these results are in line with current models of anxiety that posit decreased voluntary control of attention when levels of trait (or state, less consistently) anxiety are increased (Eysenck et al., 2007; Bishop 2009), and also with recent imaging data showing that in conditions of physical threat responses to irrelevant (neutral) information are increased (Choi et al., 2012).

At this stage, two complementing accounts could be raised, in order to explain this profound dissociation in effects of anticipatory anxiety on attention control. Stressful states are related to excessive dopamine turnover in prefrontal cortex (Arnsten 2009, for a comprehensive review), and animal studies have shown an inverted U relationship between prefrontal dopamine function and the efficiency of DA-related cognitive processes (Goldman-Rakic et al., 2000). If we assume that PST is an anxious state entailing a mild stress response, and therefore moderately enhances DA turnover in prefrontal cortex, then the processing of goal relevant stimuli may be preserved in this condition. As it turns out, psychological stressors could even exacerbate the DA-mediated prioritization of goal-relevant processing (with an increased engagement of frontal attentional control circuits regarding task-related stimuli), potentially resulting in what we observe in both the perceptual load and PST conditions, namely an efficient filtering of early neural responses in V1 to irrelevant information. However, when the prefrontal DA turnover becomes excessive, as for instance during the experience of BT, these prefrontal-based attention control systems are no

longer efficiently differentiating relevant from irrelevant information, leading to an inefficient filtering of irrelevant visual stimuli (C1 results), as well as a reduced processing of goal-relevant ones (P300 results). Alternatively, the arousal biased-competition model (ABC, Mather and Sutherland 2011) also provides good explanatory power in the present case. This cognitive model predicts that enhanced levels of arousal exacerbate "prioritization" (and hence biased competition), such that the asymmetry regarding resource allocation between relevant and irrelevant stimuli is augmented under stressful situations. Priority is based, in this model, on top-down factors such as goal-relevance, as well as bottom-up (perceptual) properties like abruptness, intensity and frequency. Moreover, emotional factors and motivational relevance also contribute to shape "priority" (for a recent review, see Ptak 2012). Translated to our new ERP findings, when participants were experiencing increased arousal and distress because their self-efficacy was transiently challenged (i.e. PST), the processing of the central, task-relevant stimuli was maximized while the peripheral, irrelevant stimuli were actively suppressed. In line with this idea, independent findings suggest increased goal shielding under acute PST (Plessow et al., 2011). By comparison, when the arousal increase could somehow be tagged to the salient aversive sounds (BT condition), these stimuli became irrepressibly prioritized during the competition for attention allocation, over the visual stimuli *tout court*. In this model, the normal competition among the two types of visual stimuli (task-relevant vs. irrelevant) is therefore altered because the artificial bottom-up saliency created by the aversive sound overrules the normal top-down prioritization of central task-relevant stimuli over peripheral irrelevant ones. Hence, the ABC framework appears valuable in explaining why under BT (unlike PST), task-relevant stimuli became less prioritized and, accordingly, they elicited a smaller P300 component, while abrupt peripheral (albeit irrelevant) stimuli were not actively filtered out in

visual cortex. Interestingly, this model is also able to account for the stronger filtering effect at the level of V1 in the PST condition as compared to the Load condition: whereas in the latter one arousal significantly habituates (thus, weakening the impact of top-down prioritization), in the PST condition arousal is maintained at higher levels, prioritizing visual processing, resulting in turn in a full-sized target-locked P300 but in a lower C1 for irrelevant stimuli.

Although our initial goal was to create two different anticipatory anxiety states, whose respective effects on attention control mechanisms could then be compared directly using a cross-over design, our experimental paradigm did not control, however, for another feature that might distinguish between these two strains, namely threat distance (Davis and Whalen, 2001). During BT, the aversive stimuli were anticipated *during* the block (thus they were unpredictable in time, but proximal), while during PST the dreaded social comparison was expected to be delivered at the end of the block (thus its occurrence was predictable to some degree, and clearly more distal). In line with this assumption, we found that SCL during PST tended to be numerically larger (relative to the control condition) towards the end of the block as compared to the beginning, suggesting that threat proximity did play a role in the emotional response to the stressor. Nonetheless, this effect could not be backed up at the statistical level because we did not have enough trials enabling to compute a reliable estimate of the changes in the SCL as a function of time. Future studies contrasting different threat types and threat proximities concurrently are therefore needed in order to further delineate the variety of changes in attention control processes concomitant to the transient experience of negative affect.

In sum, we show important dissociations between different kinds of anticipatory anxiety on attention control. The strength of our study is to characterize at the behavioral, psychophysiological and electrophysiological levels the nature and extent of these state-

dependent effects using a stringent cross-over design. Moreover, our concurrent analysis of electrophysiological responses separately for goal-relevant and goal-irrelevant stimuli reveals important dissociations that could eventually help reconcile discrepant findings on the effects of stress and anxiety on attention (hypervigilance vs. attention narrowing) reported earlier in the literature.

More generally, our results suggest an extraordinary flexibility in the ability of healthy adult human participants to readily switch from one attentional mode or affective state to the other, and in turn prioritize different parts or elements of their immediate external environment, depending on the specific goals or needs imposed by the current mind set. Futures studies are needed in order to delineate possible impairments in these dynamic and flexible attention processes, which may eventually evolve and account for specific psychopathological conditions.

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Tables and Table captions

Table I . Behavioral results: Self-report affect, Arousal levels, Reaction Times and Accuracy scores.

	VAS (mm)		SCL (μS)		RT (ms)		Accuracy (%)	
	Baseline	Test	Baseline	Test	Baseline	Test	Baseline	Test
Control	38 (4)	39 (3)	9.25 (.49)	8.96 (.52) *	588 (13)	604 (12)	94.1 (1.4)	93.3 (0.7)
Load	36 (3)	48 (4) **	9.07 (.53)	8.79 (.55) *	589 (14)	646 (17) **	95.5 (1.2)	78.5 (1.6) **
BT	38 (3)	52 (4) **	9.15 (.48)	9.88 (.54) **	594 (13)	595 (11)	95.9 (0.7)	95.2 (0.7)
PST	43 (3)	53 (3) **	9.47 (.47)	9.39 (.46)	592 (12)	583 (14)	94.9 (0.7)	95.5 (0.7)

Note. SEM values in parentheses. Abbreviations: BT = Bodily Threat; PST = Psychosocial Threat; VAS = visual analog scale; SCL = skin conductance level; RT = Reaction Times. Asterisks indicate that the values are significantly different between Baseline and Test block (* $p < .05$; ** $p < .005$).

Table II. Summary of main effects for each condition: behavioral, psychophysiological and neurophysiological.

	Behavioral indices	Peripheral arousal	Goal-relevant P300	Irrelevant Stimuli C1
Control	=	-	=	=
Load	-	-	-	-
BT	=	+	-	=
PST	=	=	=	-

Note. "=" symbol indicates no change between baseline and test; "+" indicates an increase; "–" indicates a decrease. Abbreviations: B = Baseline; T = Test; BT = Bodily Threat; PST = Psychosocial Threat.

Inline Supplementary Table I

	VAS pleasantness (mm)		VAS tension (mm)	
	Baseline	Test	Baseline	Test
Control	58 (4)	57 (4)	34 (4)	35 (4)
Load	60 (4)	49 (4) **	33 (4)	44 (4) **
BT	56 (4)	45 (5) *	32 (4)	50 (4) **
PST	54 (4)	44 (4) **	40 (4)	48 (3) *

Self-report affective state results: separate values for pleasantness and tension scores at the end of each block. SEM values in parentheses. Abbreviations: BT = Bodily Threat; PST = Psychosocial Threat; VAS = visual analog scale. Asterisks indicate that the values are significantly different between Baseline and Test block (* $p < .05$; ** $p < .005$).

Figures and figure captions

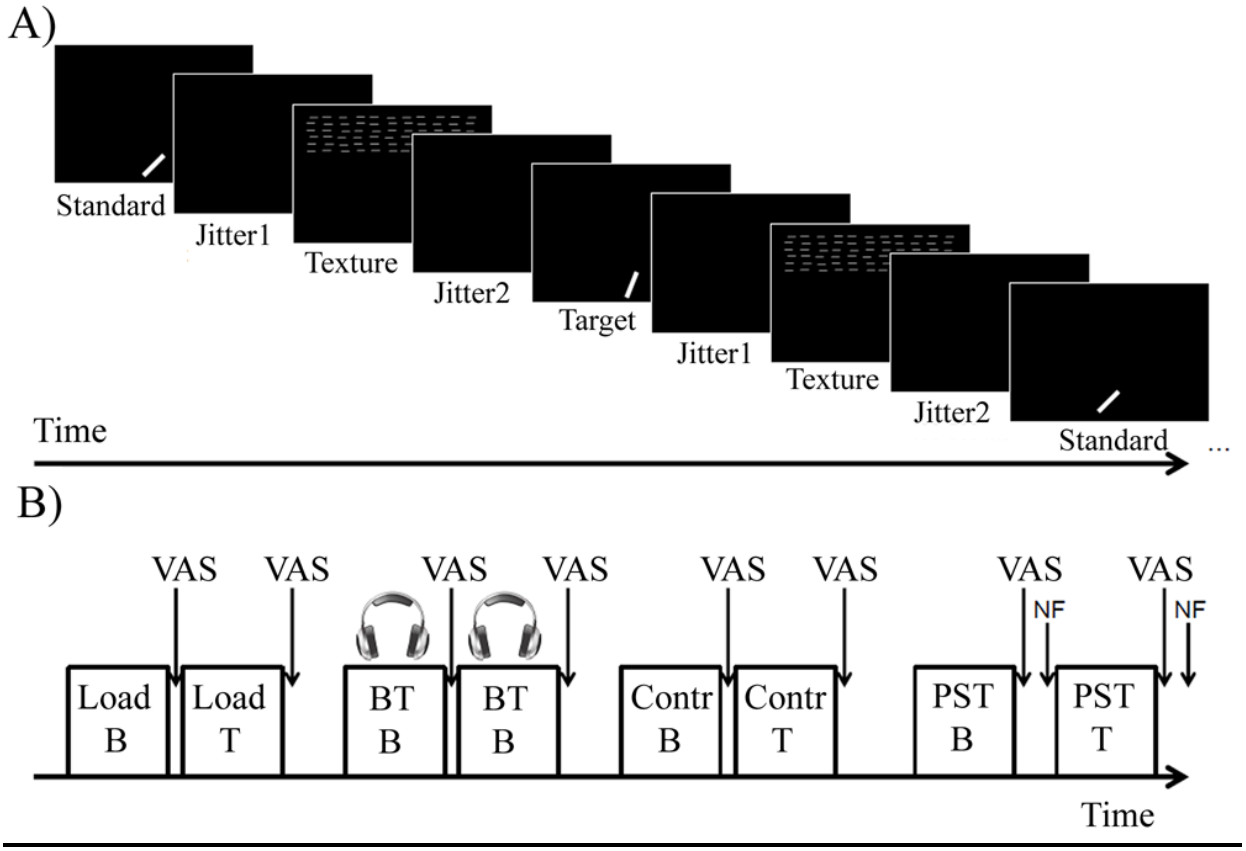


Figure 1. Task and procedure. a) Trial sequence. b) The experimental session comprised 4 conditions, each composed by two blocks (Baseline, B and Test, T). At the end of each block Visual Analogue Scales (VAS) were administered to assess distress (self reports). At the end of each block of the Psychosocial Threat (PST) condition, a comparative Negative Feedback (NF) was administered. Only during the Bodily Threat (BT) blocks, participants wore EEG-compatible earphones. Contr = Control condition.

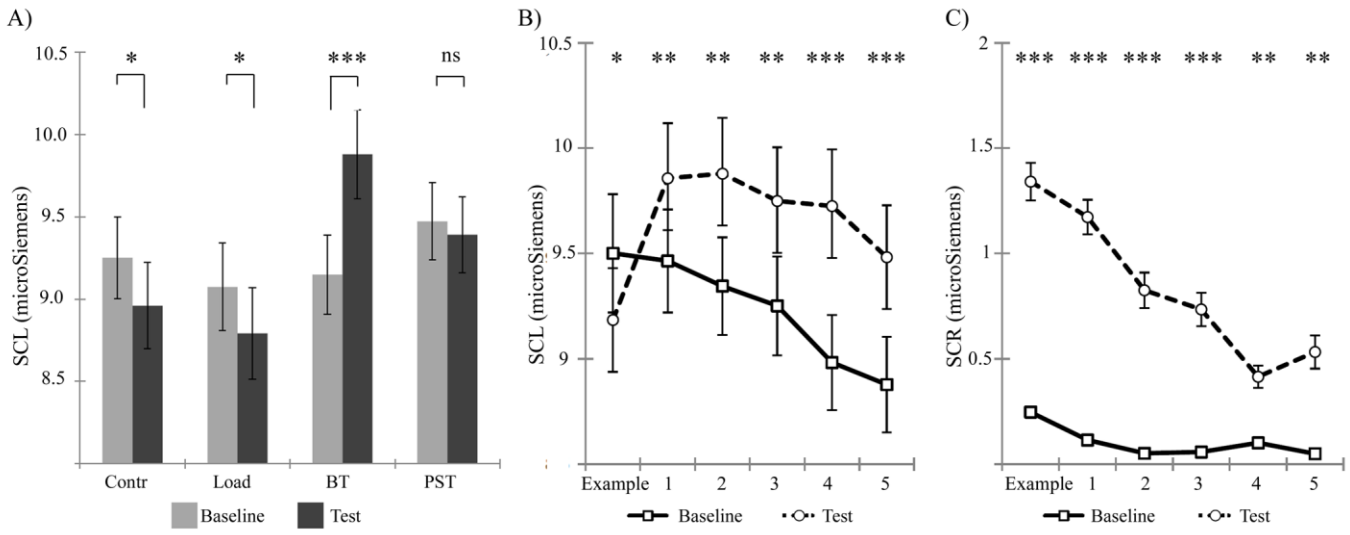


Figure 2. Skin Conductance Level (SCL) results. a) Tonic SCL measured throughout the experimental blocks. b) Pre-sound SCL (average value during the 2 seconds immediately preceding every sound delivery). c) Base-to-peak SCR in response to the safe and aversive sounds. Error bars indicate 1 SEM (note that the lack of a visible SEM for the safe sounds is explained by the near zero variability in this condition). * indicates $p < .05$; **$p < .01$; ***$p < .001$.

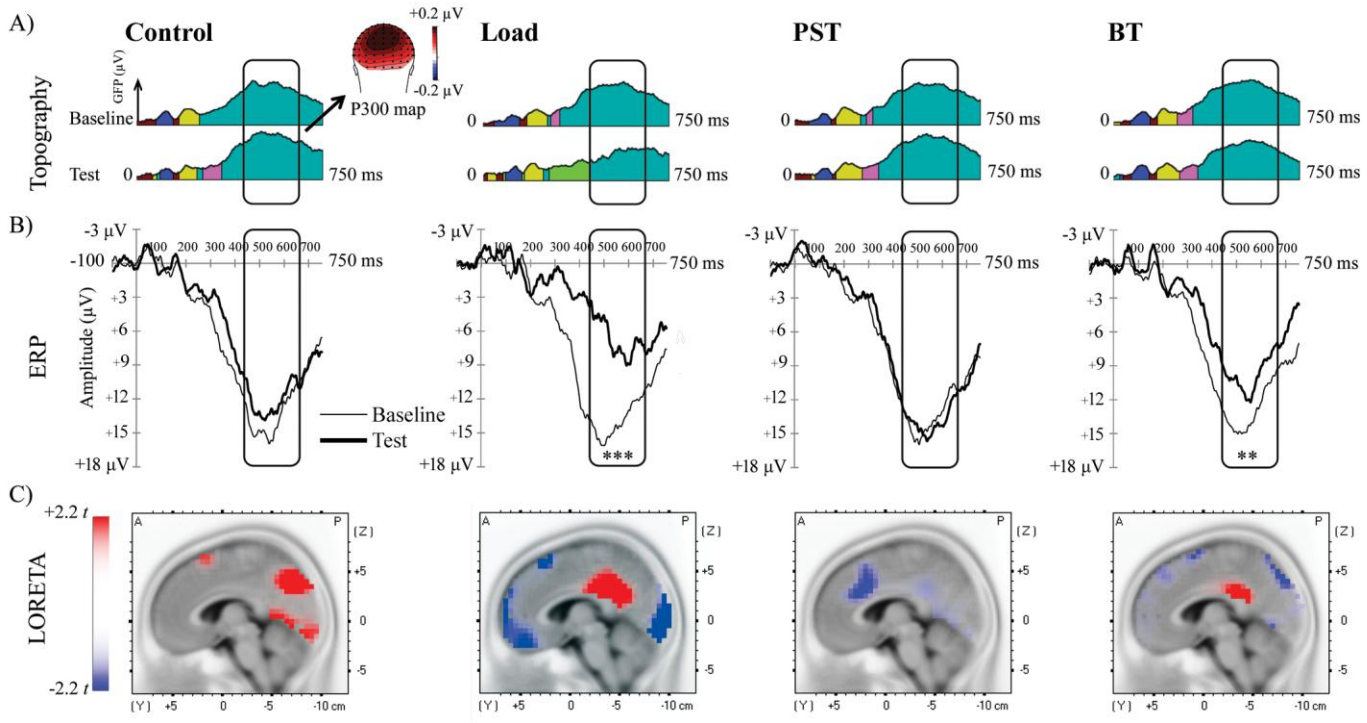
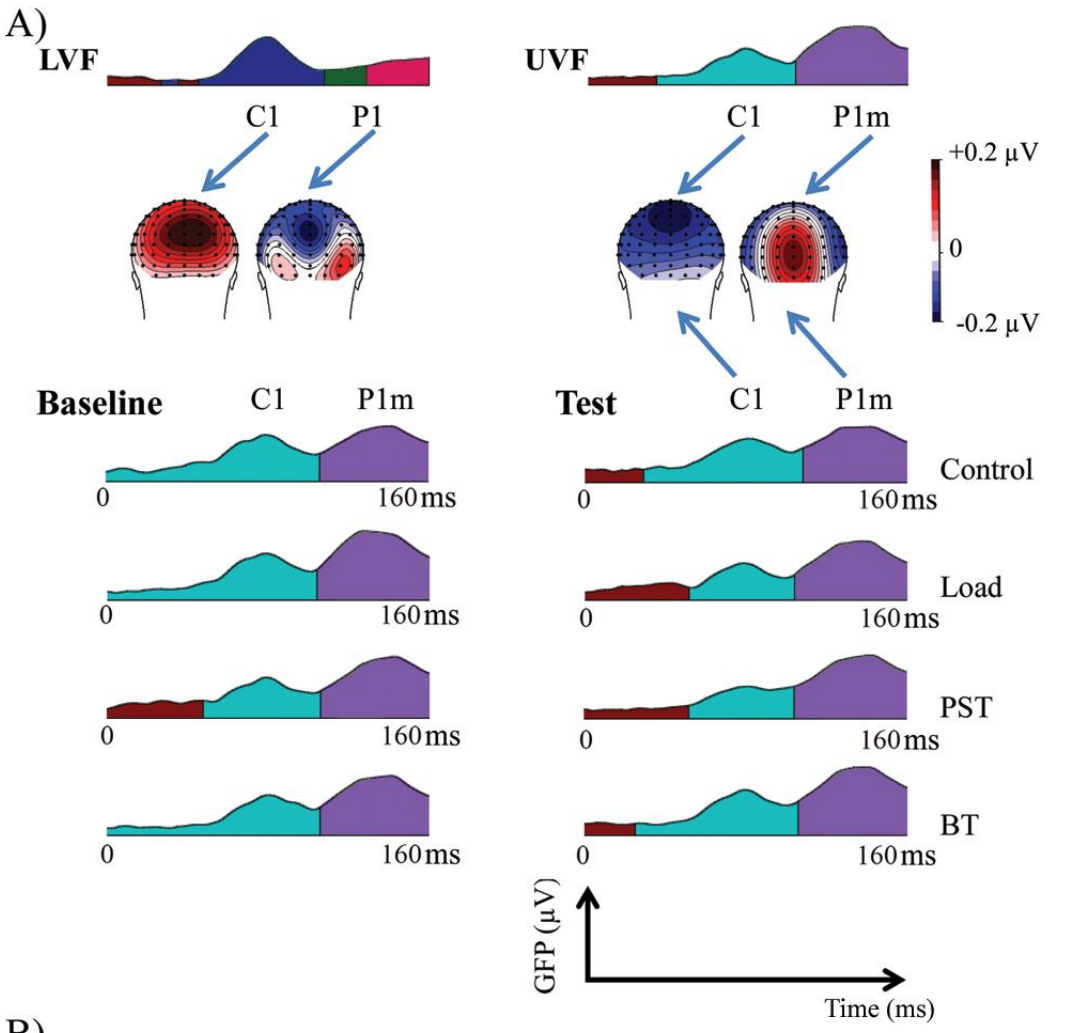


Figure 3. ERP results for goal-directed processing. Topographical analysis, ERP waveforms and Source reconstruction results (sLORETA) are depicted in a), b), and c), respectively. 3a) One dominant topographical map characterized by a monopolar parietal positivity was extracted from the segmentation of the target-locked ERPs in the P300 interval (onset 400-430 ms). 3b) ERP waveforms in response to target (oddball) stimuli pooled across the leads comprised in the analysis (A4/CPPz, A19/Pz, A20/PPOz and A21/POz). Load and BT reliably reduced the size of the P300, while merely repeating the same block (Control) or undergoing PST did not influence the magnitude of this target-related ERP component. Thin lines: Baseline Block; Thick lines: Test Block. 3c) sLORETA results (sagittal slide, +5x in Talaraich coordinates) for the time interval corresponding to the topographical and ERP analyses (430-680 ms). Only significant ($p < .05$) voxels are shown. **$p < .01$; ***$p < .001$. BT = bodily threat; PST = Psychosocial Treat.


A)
LVF
UVF
C1
P1
C1
P1m
+0.2 µV
0
-0.2 µV
Baseline
C1
P1m
Test
C1
P1m
Control
Load
PST
BT
0
160ms
GFP (µV)
Time (ms)

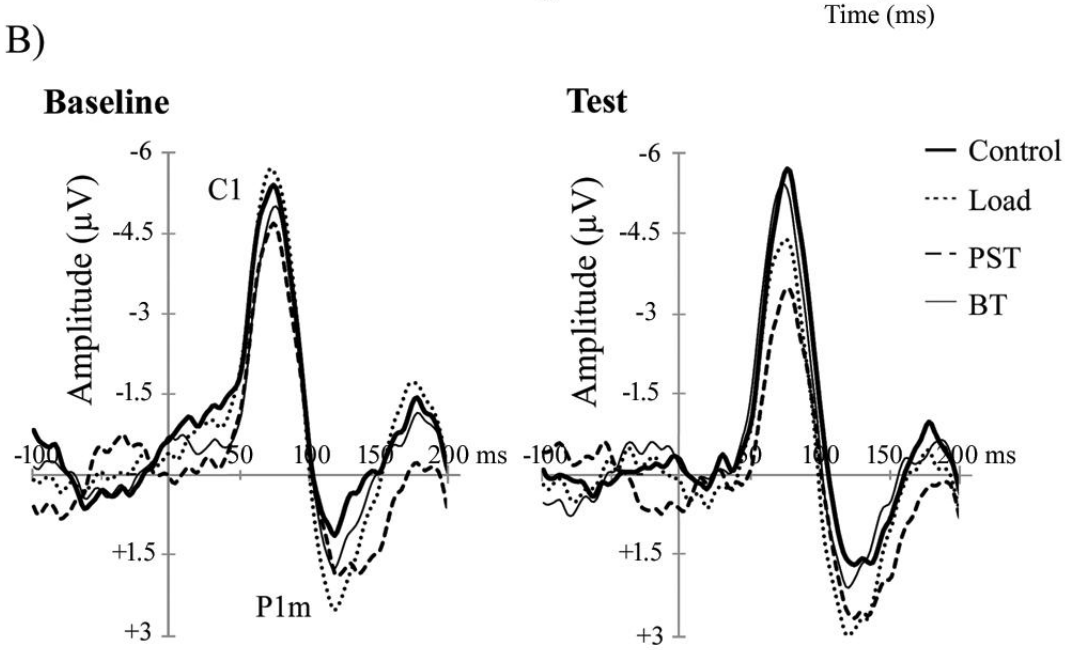

B)
Baseline
Test
Amplitude (µV)
-6
-4.5
-3
-1.5
+1.5
+3
C1
P1m
-100
50
100
150
200 ms
Control
Load
PST
BT

Figure 4. C1 results. a) Topographical analysis for the independent localizer and task blocks. A single dominant C1 map was shared across localizer and all task blocks, in response to unatteded stimuli presented in the Upper Visual Field (UVF). During the localizer, the same stimuli presented in the Lower Visual Field (LVF) elicited, at the same latency, a qualitatively different map, reflecting the diagnostic polarity reversal of this early retinotopic component. Following the C1 map, a P1 map was extracted. This component was bilaterally distributed for stimuli in the LVF, while centered around the midline (P1m) for stimuli in the upper visual field, in line with previous studies (Fu et al., 2009; Handy, Soltani and Mangun, 2001; Rossi & Pourtois, 2012a; Vanlessen et al., 2013). For each topographical map (C1 and P1), the ERP amplitude at each electrode has been normalized by the Global Field Power, following standard practice. b) ERP waveforms in response to the peripheral stimuli for the task blocks, separately for baseline (identical) and Test (critical) blocks, pooled across the leads comprised in the analysis (A4/CPPz, A19/Pz, A20/PPOz and A21/POz). BT = bodily threat; PST = Psychosocial Treat.

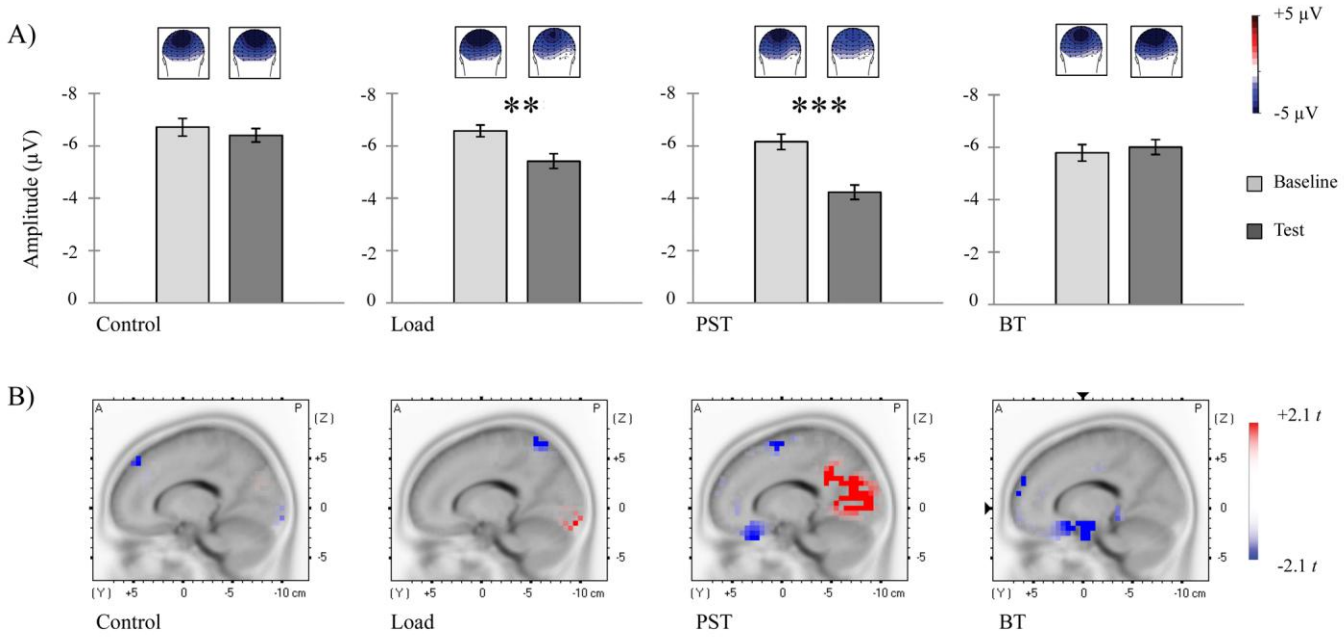
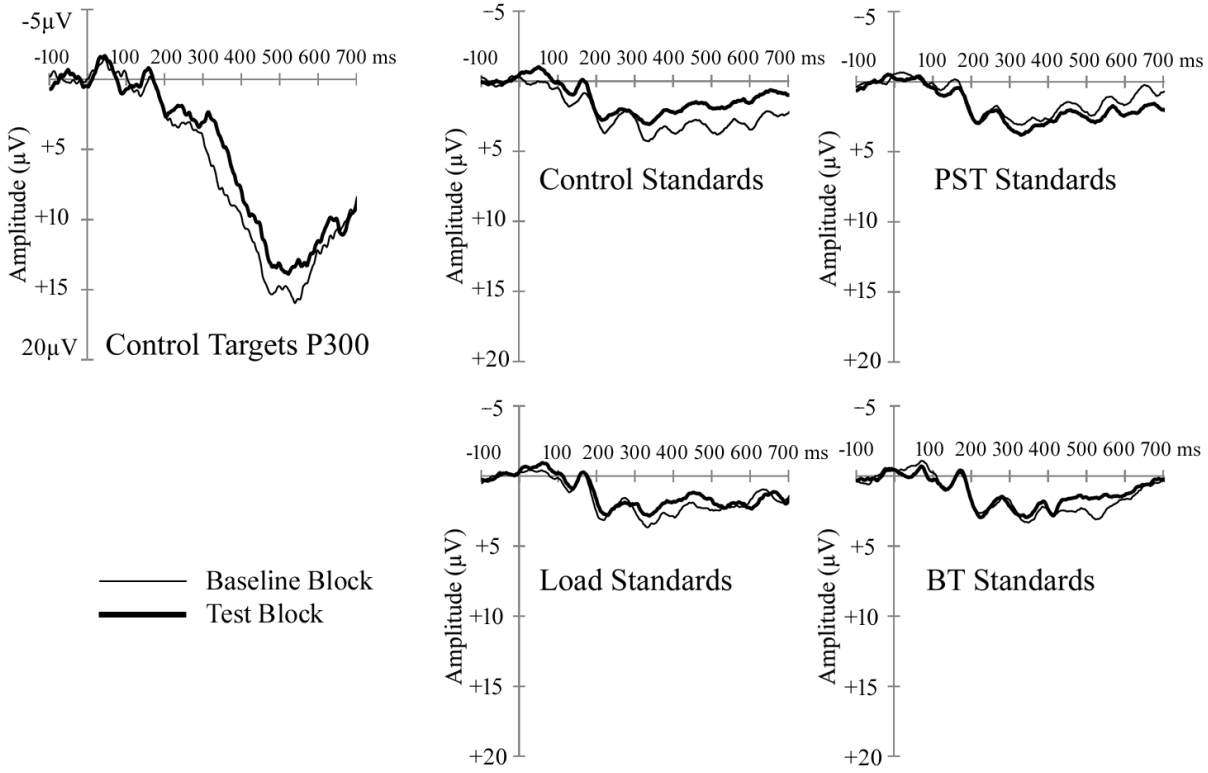


Figure 5. Source localization results for the C1. a) For each condition and block separately, C1 (peak) amplitude values (pooled across several adjacent leads, see methods), and corresponding voltage maps (latency: 75 ms). b) sLORETA results (sagittal view; x=+15 in Talaraich coordinates) for the C1 component. Only significant ($p < .05$) voxels are shown. Error bars indicate 1 SEM. ** indicates $p = .005$; ***$p < .001$. Abbreviations: BT = bodily threat; PST = Psychosocial Treat.



Inline Suplementary Figure 1. ERP waveforms in response to standard stimuli. ERP waveforms in response to standard (80% of the total central) stimuli, pooled across the leads comprised in the analysis (A4/CPPz, A19/Pz, A20/PPOz and A21/POz). For comparison, the ERP response to Target stimuli in the control condition is presented in the left panel. In the Control condition, the amplitude of the ERP response to the standard stimuli was significantly decreased when moving from Baseline to Test block. In all other conditions this comparison was non-significant. Thin lines: Baseline Block; Thick lines: Test Block.