



Contents lists available at ScienceDirect



Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Someone's lurking in the dark: The role of state anxiety on attention deployment to threat-related stimuli

Valentina Rossi*, Gilles Pourtois

Psychopathology & Affective Neuroscience Laboratory, Department of Experimental-Clinical and Health Psychology, Ghent University, Belgium

ARTICLE INFO

Article history:

Received 12 May 2015

Received in revised form 30 October 2015

Accepted 31 October 2015

Available online xxx

Keywords:

State anxiety

Attentional scope

Hypervigilance

Bias

ERPs

C1

Load

Stress

ABSTRACT

Anxious states can alter attention, impairing goal-directed processing in favor of bottom-up capture. However, it is still unclear whether anxiety-related biases already influence the earliest stage of information processing, especially for unattended threat-related stimuli.

Here we tested, using EEG, if the amplitude of the first component of the Visual Evoked Potentials (C1) to simple visual stimuli (either neutral or threat-related) varied depending on anxiety level and task demands.

Results showed that anxiety altered goal-directed processing, reducing P300 amplitude to target stimuli, while it increased the C1 to irrelevant stimuli, regardless of their emotional content. Moreover, enhanced load at fixation reduced the amplitude of this component to neutral stimuli, but this early filtering effect was abolished by state anxiety.

These results shed light on the time-course of attentional biases in anxiety, confirming that this transient state can enhance bottom-up capture as early as in V1, at the expense of goal-directed processing.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Imagine walking alone, late in the evening, in an outdoor parking lot. Suddenly, an alarm goes off, and you startle irreversibly. In this context, the previously non-threatening dark edges of the parking space become possible locations for attackers, and you automatically start looking out for menacing individuals. A simple abrupt sound has unlocked a fear reaction, which will prepare the organism for a fight or flight response. In the next few days, the simple idea that in the evening you will have to visit that parking lot again might elicit an unjustified state of enhanced arousal, accompanied by nervousness and worries about your safety: this constellation of affective, cognitive and physiological changes in response to a distal threat can be identified as "state anxiety" (Spielberger, 1983).

1.1. State anxiety and task demands

Previous studies showed that state anxiety interferes with cognition, altering the allocation of attention and cognitive resources. For example, being in a situation in which one might receive an elec-

tric shock has been shown to mobilize cognitive resources from a goal-directed to a bottom-up processing style (Shackman, Maxwell, McMenamin, Greischar, & Davidson, 2011), and increase sensitivity to emotional distraction (Robinson, Vytal, Cornwell, & Grillon, 2013). While effects of state anxiety on low-demand tasks have been reported mainly at the level of post-perceptual processing (P300 component of the Event Related Potentials, ERPs), it has been suggested that the interference of anxiety on cognitive processing diminishes when task demands are increased (Hu, Bauer, Padmala, & Pessoa, 2012; Vytal, Cornwell, Arkin, & Grillon, 2012). This leads to the prediction that while in low demand tasks the effects of state anxiety will be detectable, in highly demanding task the goal-directed processing might be relatively spared. Moreover, this could suggest that the attentional capture by emotional distractors (attentional bias), that is observed at low load during anxious states, might be hampered or abolished by high load tasks, resulting in better filtering of irrelevant emotional information (basically, restoring normal attentional effects).

1.2. State anxiety and attention to emotional information

Interestingly, it is still highly debated to what extent the processing of emotional aspects of stimuli is attention-dependent (e.g., Everaert, Spruyt, Rossi, Pourtois, & De Houwer, 2013; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002), and therefore under

* Corresponding author at: Department of Experimental-Clinical and Health Psychology, Ghent University, Henri Dunantlaan 2, 9000 Ghent, Belgium. Tel.: +32 9 264 6472; fax: +32 9 264 6472.

E-mail address: valentina.rossi@ugent.be (V. Rossi).

which attention conditions emotional stimuli could bypass the sensory filtering that task demands impose to the sensory system. In other words, are there specific emotional stimuli that can elicit strong responses early on in the sensory stream, even when attention is depleted by a competing high load task? When dealing with neutral, non social stimuli, increasing attentional load at fixation typically decreases the sensory responses to irrelevant information throughout the visual processing pathways, starting from the primary visual cortex (V1; Lavie, 2005; Rees, Frith, & Lavie, 1997; Schwartz et al., 2005). In the electrophysiological domain, the earliest effects of load have been reported for neutral stimuli around 75 ms after stimulus onset, at the C1 level (Rauss, Pourtois, Vuilleumier, & Schwartz, 2009; Rauss, Pourtois, Vuilleumier, & Schwartz, 2012). The C1 is the first visual electrophysiological component, and it is classically considered arising from V1 (Foxe & Simpson, 2002; Jeffreys & Axford, 1972; Rauss, Schwartz, & Pourtois, 2011). Concerning this very early stage of sensory processing, it remains unresolved if early gating effects at the C1 latency (i.e., load-related narrowing of the focus of attention, reflected in a reduction of the C1 responses to irrelevant stimuli concurrently presented in the visual field) could also be observed when the competing stimuli contain threatening, biologically-relevant information. Moreover, it is still undetermined if state anxiety can have an impact on this attentional filtering at such an early latency during sensory stimulus processing.

A sensory bias for emotional stimuli on the C1 amplitude has been reported in neutral emotional states for negatively conditioned stimuli (Stolarova, Keil, & Moratti, 2006), and for fearful faces (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; West, Anderson, Ferber, & Pratt, 2011). However, in these earlier studies, task demands were not manipulated, leaving open the resource-dependency of these effects. On the other hand, load-related costs on emotional information processing are mainly investigated in limbic structures (amygdala) and frontal cortex using neuroimaging techniques (Vuilleumier, 2005). Crucially, these effects of load on emotion processing seem to be moderated by state and trait anxiety (Bishop, Jenkins, & Lawrence, 2007; Dvorak-Bertsch, Curtin, Rubinstein, & Newman, 2007), with higher anxiety levels being related to more pervasive threat processing advantages (Cornwell et al., 2011). Surprisingly, even though attention, emotional content and state anxiety are all crucial factors modulating early sensory

gating (for a review, Vuilleumier, 2015), no study to date has addressed their putative interaction effects in lower-tier visual cortex.

1.3. State anxiety and early sensory processing

In fact, most of the previous studies investigating the effects of load on emotional stimulus processing did not take into account levels of state anxiety in the participants, and mostly focused on ERP components generated at later stages of processing (e.g., EPN or LPP, e.g., Schupp et al., 2004). Some indirect indications concerning the effects of anxiety on V1 come from a recent study (Weymar, Keil, & Hamm, 2014) in which the C1 amplitude was contrasted in spider-fearful and control participants. In their study, Weymar et al. showed that the C1 for all types of stimuli (threat-related and neutral) was increased in spider-fearful participants, interpreting this effect as generic hypervigilance, which increases sensitivity to all incoming sensory stimuli (regardless of their threat value) in order to swiftly detect potential threat in the environment (Somerville, Whalen and Kelley, 2010). Using neutral stimuli, Shackman et al. (2011) also demonstrated that state anxiety induced through threat of shocks increases early sensory processing (at the N1 level), impairing later, goal-relevant processing (P300). We recently confirmed P300 reductions due to state anxiety, but we also showed how the C1 to neutral stimuli could be either decreased by load and by a state of anxiety related to rumination, while maintained during anxiety related to hypervigilance (Rossi & Pourtois, 2012a, 2014). However, our recent ERP studies did not involve emotional stimuli, leaving important questions, concerning the actual relationship between anxiety levels and specific threat-related biases in V1, still open.

1.4. Rationale for the current study

Therefore, in the current study we manipulated attentional load, anxiety levels and stimulus content concurrently to address this open issue. Crucially, we used a multi-measure approach to ascertain that our load manipulation was effective in consuming cognitive resources (behavior and P300 amplitude), and that our induction protocol efficiently increased state anxiety (by monitoring the psychological and physiological state of the par-

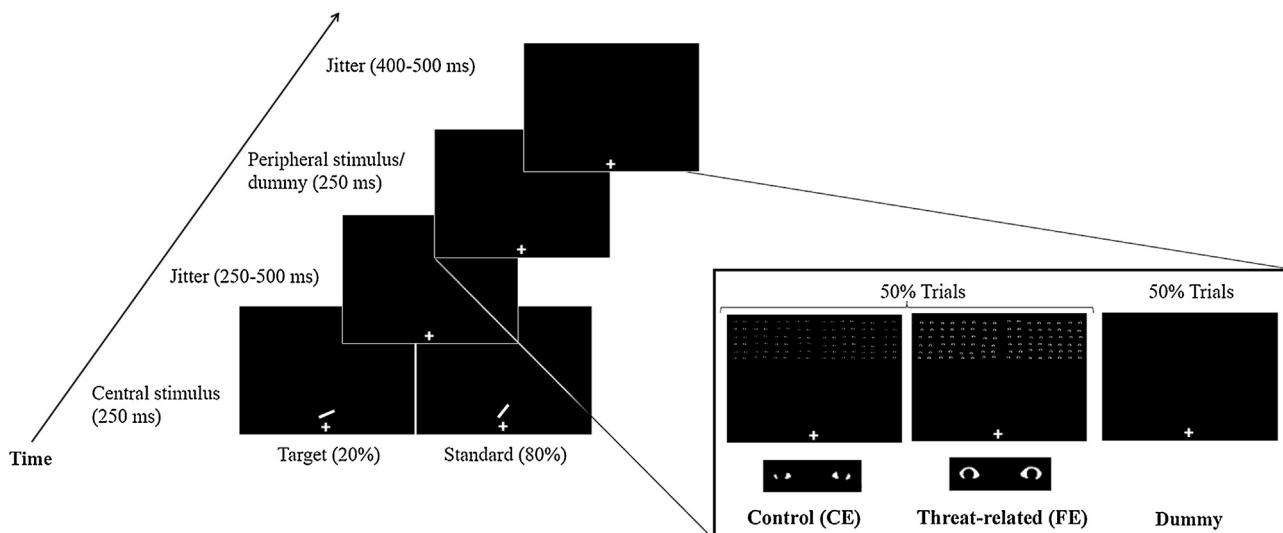


Fig. 1. Trial structure.

A prototypical trial was composed by a central stimulus (standard or target, 250 ms), a jittered interval (250–500 ms), a peripheral irrelevant stimulus or a dummy (250 ms) and a second jittered interval (400–500 ms). The peripheral stimuli (shown in the upper visual field), presented only in 50% of the trials, were textures composed by pairs of eye-whites (Control Eyes, CE, and Fearful Eyes, FE). Stimuli are not depicted to scale.

ticipants through self-report distress scores and electrodermal activity, respectively). Moreover, with our design we are able to concurrently measure goal-directed processing (behavior and brain responses to the relevant foveal stimuli) as well as attentional narrowing/hypervigilance (C1 to peripheral irrelevant stimuli), in such way that anxiety-related cognitive biases towards one or the other could be thoroughly characterized.

First, we predicted impairments in goal-directed post-perceptual processing during anxiety (P300 component, Moser, Hajcak, & Simons, 2005; Shackman et al., 2011), with similar effects to increased load. Second, to be able to capture attention and anxiety effects in V1 at the level of the C1 component, we constructed socially relevant threatening stimuli consisting in widespread arrays of human eye-whites (extracted from a fearful or a control face), and presented them on a black background. Eyes (and in particular the eye-whites) have been shown to play a predominant role in fear processing (Ahs, Davis, Gorka, & Hariri, 2014; Schyns, Petro, & Smith, 2007), and engage the defensive system (Whalen et al., 2004), especially when particularly salient (Mothes-Lasch, Mentzel, Miltner, & Straube, 2013). We therefore tested whether this type of biologically relevant emotional material would be more resistant to early attentional filtering during a competing high load task, as compared to non-threatening control stimuli. Furthermore, combining our load manipulation, an anxiety induction and the use of threatening stimuli, we could test whether state anxiety would elicit generic sensory hypervigilance already in early visual cortex depending on the concurrent attentional demands, or rather induce a more specific sensitivity to threat.

2. Methods

2.1. Participants

Twenty-eight undergraduates took part in the study for monetary compensation. Two participants were excluded from the analyses (one did not complete the experimental session, and one had continuous slow drifts in the EEG, impairing the recorded signal), resulting in a sample of 26 participants (mean age = 22.3 years, SD = 2.7, 6 males). Participants had normal or corrected-to-normal vision, were unaware of the purpose of the study, were not under psychoactive medication and declared no history of psychiatric or neurological disorders. 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 stimuli, oddball task parameters and anxiety induction procedure were based on the methods used previously in Rossi and Pourtois (2014). Participants were required to keep their eyes on the fixation cross shown on screen, and to respond with a key-press (right index finger) to deviant visual stimuli (targets, 20%) randomly intermixed in a stream of standard stimuli (80% of the total), which did not require any manual response. Both standard and target stimuli consisted in tilted line segments presented one by one, just above the fixation cross. Standard lines were tilted 35° with respect to the horizontal meridian, while targets had a different in-plane orientation (45° or 25° in the blocks where the load level was low, 32° or 38° where load was high). A prototypical trial is depicted in Fig. 1. Irrelevant stimuli, presented in the periphery of the upper visual field (UVF) only in 50% of the trials, were textures composed by pairs of eye-whites (modified after Whalen et al., 2004). To test for differential attention allocation to neutral and threatening information, in half of the cases the peripheral textures were composed by eye pairs taken from a happy face (Control

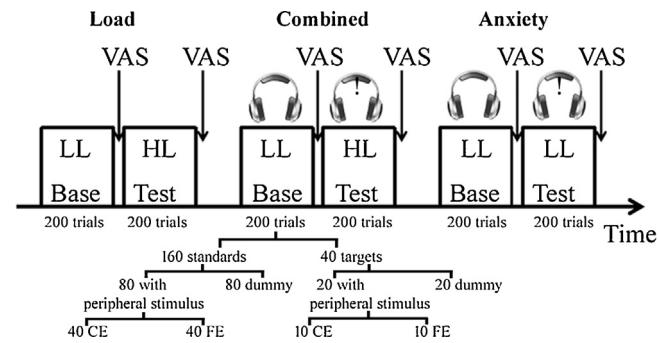


Fig. 2. Procedure.

Conditions were fully randomized across participants, while block order (baseline, test) was fixed. Each block consisted in 200 trials, and the stimulus subdivision (160 standards, 40 targets etc.) was identical across blocks and conditions.

Eyes, CE), and in the other half from a fearful face (Fearful Eyes, FE, see Whalen et al., 2004).

In order to experimentally induce state anxiety, we used aversive auditory stimuli (Hintze, Junghofer & Bruchmann, 2014; Robinson et al., 2013; Rossi & Pourtois, 2014). Participants were informed that they might receive, through EEG-compatible insert earphones (3M E-A-RTONE-3A, 10 ohm), some task-irrelevant sounds (see procedure). Selectively in some blocks these sounds were aversive white noise bursts (Threat Sound, 100 dB, 50 ms duration). In other blocks, used as control (safe) conditions, the sounds were instead a low-volume, non-threatening sine wave (Safe Sound, 1000 Hz, 60 dB volume, 200 ms duration). Sounds ($N=5$ per block) were never predictive of target or standard stimuli, and they were presented in five additional inter-stimulus intervals (750 ms), randomly distributed during the blocks (inter-sound-interval range: 26–119 s).

2.3. Procedure

Participants signed an informed consent form, completed the first self-report measure of state anxiety (STAI-S, 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 (DELL monitor, refresh rate 100 Hz). Initially, they received instructions on the visual oddball detection task and completed two short practice blocks (one for low load, one for high load, 24 trials per block), during which the experimenter closely monitored their performance. If needed, the practice blocks were repeated; after reaching acceptable performance during the practice, participants moved on to the task blocks. Each of the six blocks of the detection task comprised 200 trials (40 targets, 160 standards). Of these 200 trials, 100 entailed also a peripheral stimulus; the other half contained a dummy (see Fig. 1, inset). Unknown to the participants, the six blocks were divided into three conditions, each composed by a Baseline Block and a Test Block (see Fig. 2): Load, Anxiety, and their Combination. Participants were instructed that if (and only if) they received an example of a sound before a given block, they might receive again the same sound unexpectedly during the immediately following block. In the Load condition, no sounds were ever presented; the Baseline block was Low Load (LL), and the Test block was a High Load (HL) block. In the Anxiety condition both blocks were low in attentional load. The Baseline block contained only Safe sounds, while in the Test Block, unpredictably, Threat Sounds were delivered, causing a defensive response (as detected in the galvanic skin response) and increased state anxiety (captured at the self-report level). In the Combined condition, the Baseline block was again a low load block with Safe Sounds, while the Test block consisted in a high load block with Threat Sounds (thus, it was

a combination of the other two manipulations, with both a state anxiety induction and a highly taxing perceptual task). The order of the three conditions was fully counterbalanced across participants. Using this procedure, each manipulation had its respective Baseline Block, used as reference for the statistical analyses, in such a way to control for undesired time effects (see also Rossi & Pourtois, 2014 for a similar procedure). In addition, in our design the order of Baseline and Test blocks was not counterbalanced, in such a way that the Baseline block always preceded the crucial Test blocks, buffering for any lingering carryover effect (already limited by the instructions that preceded every pair of blocks). Crucially, in all blocks and conditions the peripheral stimuli remained identical, allowing their direct comparison at the ERP level.

To capture levels of distress at several points in time, participants were also asked to report, using two horizontal, digital Visual Analog Scales (VASes, pleasantness and tension), their subjective affective state after each block (six times in total). The two VASes (that were, as expected, significantly correlated in this sample: range $r = -.29$ to $r = -.60$; median $r = -.57$, $p < .01$), were then combined in a compound score of distress to increase reliability.

At the end of the experimental session, participants completed two more blocks in passive viewing conditions, used as an independent localizer for the C1 component in response to the peripheral stimuli, which were presented in random fashion in the Upper and Lower Visual fields (UVF, LVF; see Rossi & Pourtois, 2014; Vanlessen, Rossi, Raedt, & Pourtois, 2014). Using these blocks, we ascertained that the two types of peripheral stimuli (CE and FE), elicited statistically equivalent C1 responses. In addition, during the localizer, a third type of stimulus was also presented, randomly intermixed with the two types of eye stimuli used in the main task. This extra stimulus was a texture composed of horizontal line segments, comparable in size to the CE and FE, but not social in nature, and neutral in valence (see Rossi & Pourtois, 2014 for similar procedures). Also this stimulus type elicited C1 responses that were not statistically different from the two eye-based textures.

Finally, participants filled out a second State Anxiety Inventory (STAI-S) and three additional trait-related questionnaires: STAI-T (Spielberger, 1983); BIS/BAS (Carver & White 1994); RRS, Rumination Response Scale (Nolen-Hoeksema & Morrow 1991). Just before leaving the experimental room, participants were asked questions about the peripheral stimuli they were presented with (in order to probe awareness of their content). They were shown one example of each type of stimuli used in the task and localizer (texture of lines, CE and FE) and asked to rate them on a Likert scale for valence (1/negative-7/positive) and arousal (1/neutral-7/arousing, exciting). Last, they were debriefed and compensated for their participation.

2.4. Electrophysiological data recording and reduction

EEG was recorded from 128 active Ag/AgCl electrodes evenly distributed over the scalp surface using an elastic cap (ABC layout, Biosemi ActiveTwo System). The continuously recorded EEG signals were online referenced to the CMS–DRL ground (driving the average potential across the montage as close as possible to the amplifier zero, <http://www.biosemi.com>), 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 connected to the same amplifier as the EEG electrodes (Biosemi ActiveTwo 24-bit AD-box) were applied to the volar surfaces of the medial phalanges of the left index and mid-

dle fingers in order to record the Skin Conductance Levels (SCL) throughout the experimental session.

Signals were analyzed as recommended in recent guidelines (Amodio, Bartholow, & Ito, 2014; Keil et al., 2014), using Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany). The continuous EEG signals were offline referenced to the linked mastoids and band-pass filtered (Butterworth 0 phase filters) between .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 and a 800 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, Coles, & Donchin, 1983). Individual epochs were baseline-corrected using the entire pre-stimulus interval, and epochs affected by residual artifacts were semi-automatically rejected on the basis of an absolute voltage criterion (± 100 μ V, average rejected trials 14.65%). 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, resulting in 6 waveforms for the central targets (Load-Baseline; Load-Test; Anxiety-Baseline; Anxiety-Test; Combined-Baseline; Combined-Test) and in 12 waveforms for the peripheral stimuli (Load-Baseline; Load-Test; Anxiety-Baseline; Anxiety-Test; Combined-Baseline; Combined-Test for the CE and the same conditions for the FE). The data of three participants were contaminated by high amplitude alpha throughout the experiment, although their performance clearly indicated that they were focused on the task. Although these alpha fuses had a negligible effect on the measurement of the long latency P300 component (which was based on a longer time interval that comprised more than one alpha cycle), these artifacts clearly fell in a similar band as the C1 component, impairing the quality of the data and making the peak measurements unreliable. We have therefore excluded these three datasets from the C1 analyses, which are then based on 23 participants.¹

ERP waveforms obtained from the six task blocks were computed separately. For the independent localizer block, ERPs in response to the peripheral textures (FE, CE and neutral lines) presented either below or above fixation (6 resulting conditions: UVF-FE; UVF-CE; UVF-lines; LVF-FE; LVF-CE; LVF-lines) were pre-processed and averaged separately, using the same parameters as for the active task blocks.

Based on previous literature (Fu, Fedota, Greenwood, & Parasuraman, 2012; Rauss et al., 2009, 2012; Rossi & Pourtois, 2012a, 2014) we performed a peak analysis for the C1 component in response to CE and FE during the six test blocks. The C1 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 parieto-occipital midline leads A4/CPz, A19/Pz, A20/PPOz and A21/POz, A22/POOz and A23/Oz.

In order to confirm the expected changes in goal-directed processing as a function of load and anxiety, we analyzed amplitude

¹ As an alternative approach to circumvent the problems posed by the alpha noise superimposed on the C1, the data for these three participants (participant number 12, 20 and 28) were additionally filtered prior to segmentation, with the goal to attenuate the alpha fuses (with a Band Rejection filter, Frequency = 10 Hz, Bandwidth 4 Hz, Order = 2). Then all the C1 analyses were performed again including these three participants, and besides small variations in the F values, the results were unchanged.

variations of the P300 component in response to correctly identified target stimuli. Based on earlier ERP studies (Kim, Kim, Yoon, & Jung, 2008; Rossi & Pourtois, 2014; Sawaki & Katayama, 2007; Shackman et al., 2011; Vanlessen, Rossi, Raedt, & Pourtois, 2013) and the topographical properties of the current data set (that showed a positive parietal distribution peaking between 500 and 550 ms across all the six conditions), we analyzed the P300 with a mean amplitude analysis (400–650 ms), at centro-parietal-occipital leads (A4/CPz, A19/Pz, A20/PPOz and A21/POz) along the midline, where this component peaked in the grand averaged data.

2.5. Data analysis

All statistical analyses were performed using SPSS (IBM SPSS statistics, v22.0.0.0).

C1 peak and P300 mean amplitude scores were analyzed separately by means of repeated measures ANOVAs. For the P300 analysis, the within-subject factors Condition (Load, Anxiety, Combined), Block (Baseline, Test) and Lead (4 levels, CPPz to POz), were included in the analysis. For the C1 analysis, the within-subject factors Condition (Load, Anxiety, Combined), Block (Baseline, Test), Lead (6 levels, from CPPz to Oz) and Eye Type (Control, Threat-related) were included in the ANOVA. Significant interaction effects were followed up by ANOVAs carried out separately for each Condition.

The SCL signals were segmented into six epochs, each encompassing the duration of one block (286 s). The average SCL values in these windows were extracted and analyzed with a 3 (Condition) \times 2 (Block) repeated measures ANOVA. Given that a phasic Skin Conductance Response (SCR) was systematically detected in response to the aversive sounds in the Anxiety and Combined test blocks, we also performed a control analysis correcting the tonic SCL values in the Anxiety and Combined conditions for the phasic SCRs. For each participant, we extracted the SCL in windows of 15 s before the delivery of each sound (in such a way that even with the shortest possible ISI, which was 26 s, this window would not encompass the SCR to the previous sound). We then averaged those 5 windows together to obtain an SCR-free value of SCL (SCL_{corr}), separately per Condition and Block. We then submitted these SCL_{corr} values to the same analysis as the original uncorrected SCL. In order to better characterize the temporal unfolding of the tonic and phasic galvanic skin response (i.e., to test if arousal habituated completely, or if it remained significantly enhanced even towards the end of the anxiety induction blocks), we performed additional analyses on SCL and SCRs, that can be found in the Supplementary materials.

Changes in affective state at the subjective level 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 & Pourtois 2012b, 2014). Therefore, higher scores (range 0–200) indicate higher levels of distress.

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.

The valence and arousal ratings for the peripheral stimuli were analyzed separately with one-way repeated measure ANOVAs with stimulus type as factor (Lines, FE, CE).

Behavioral measures (RTs, Accuracy) and self-report affect scores were analyzed with repeated measures analyses of variance (ANOVAs) with Condition and Block as within-subjects factors. A Greenhouse-Geisser correction was applied when sphericity was violated.

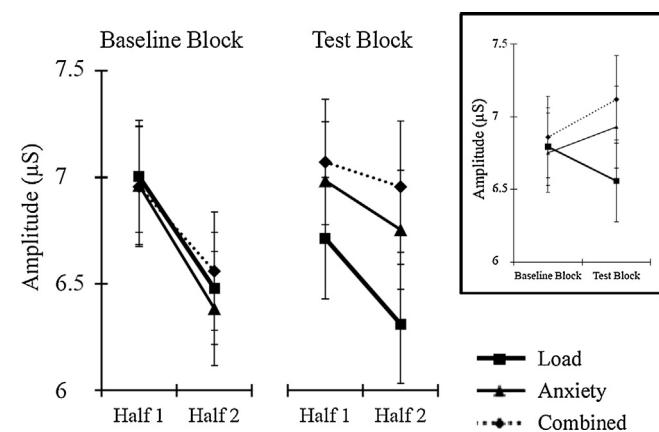


Fig. 3. Physiological arousal reaction.

Inset: SCL over the entire block (4 min). Error bars indicate one standard error of the mean.

3. Results

3.1. Behavioral data and affective response (detailed results in Supplementary Table I and II)

3.1.1. Reaction times (RTs) and accuracy

The ANOVA on the RT data (correct target detections) resulted in a main effect of Condition ($F_{2,50} = 3.35, p = .04, \eta_p^2 = .12$), Block ($F_{1,25} = 36.34, p < .01, \eta_p^2 = .59$) and a significant Condition \times Block interaction ($F_{2,50} = 4.27, p = .02, \eta_p^2 = .15$). As can be seen in Table 1, in all conditions RTs were higher in the Test block as compared to the baseline one (Load $F_{1,25} = 20.50, p < .01, \eta_p^2 = .45$; Anxiety $F_{1,25} = 6.47, p = .02, \eta_p^2 = .21$; Combined $F_{1,25} = 28.50, p < .01, \eta_p^2 = .53$). However, as the effects size suggests, the cost for the exposure to perceptual Load (both in the pure and in the combined conditions) was significantly higher than the cost elicited by the Anxiety manipulation (see Table 1). Moreover, there was no indication of an additive effect in terms of speed cost of the two strains when combined (the Pure Load and Combined conditions were not different from each other: $t_{25} = .75, p = .46$). A very similar pattern was observed for the accuracy data: the ANOVA resulted in a main effect of Condition ($F_{2,50} = 38.77, p < .01, \eta_p^2 = .61$), Block ($F_{1,25} = 133.21, p < .01, \eta_p^2 = .84$) and a significant Condition \times Block interaction ($F_{2,50} = 37.58, p < .01, \eta_p^2 = .60$). In all conditions the accuracy was higher in the Baseline as compared to the Test block (Pure Load $F_{1,25} = 100.43, p < .01, \eta_p^2 = .80$; Anxiety $F_{1,25} = 12.99, p = .01, \eta_p^2 = .34$; Combined $F_{1,25} = 81.65, p < .01, \eta_p^2 = .77$), but see Table 1 for the relative size of these differences.

3.1.2. Affective response: self-report

The ANOVA on the compound VAS scores resulted only in a main effect of Block ($F_{1,25} = 33.27, p < .01, \eta_p^2 = .57$), indicating that distress was significantly higher after the Test block as compared to the Baseline block (see Table 2, upper panel, and Supplementary Table II for further details concerning the two separate scales for Tension and Pleasantness, which showed similar patterns of results).

3.1.3. Affective response: SCL

The SCL data (see Fig. 3 and Table 2, lower panel), expressing peripheral arousal levels, complemented the results obtained at the self-report level. The signal was lost for one participant halfway during the HL block, therefore the SCL and SCR analyses were calculated based on a sample of 25 participants. The repeated measures ANOVA on the full block SCL (286 s) resulted in a significant Condition \times Block interaction (Fig. 3, inset; $F_{2,48} = 9.19, p < .01, \eta_p^2 = .28$). Importantly, no difference across conditions was

Table 1

Behavioral performance.

	RT baseline	RT test	RT difference	Accuracy baseline	Accuracy test	Accuracy difference
Load	596 (58)	657 (67)	60 ms ^{**}	94.9 (3.5)	84.9 (5.7)	10.0% ^{**}
Anxiety	598 (60)	620 (55)	22 ms [*]	95.3 (3.2)	93.7 (3.3)	1.6% ^{**}
Combined	603 (44)	652 (62)	50 ms ^{***}	94.8 (3.9)	85.4 (5.1)	9.4% ^{***}

Note. RT (reaction times) expressed in ms (S.D.) and accuracy, expressed in percentage (S.D.) during baseline and test blocks for the three experimental conditions. As can be seen from the RT difference scores, the cost for pure load and for the combined condition were similar (load vs. combined, $t_{25} = .75$, $p = .46$), and both significantly higher than the cost elicited by pure anxiety ($t_{25} = 2.53$, $p = .02$ and $t_{25} = 2.42$, $p = .02$, respectively). The same applies to the accuracy data: the costs for pure load and combined are significantly higher than the cost elicited by the anxiety condition (comparing delta scores, pure anxiety vs. load $t_{25} = 7.27$, $p < .01$; pure anxiety vs. combined $t_{25} = 6.91$, $p < .01$; load vs. combined $t_{25} = .64$, $p = .43$).

^{*} $p < .05$.^{**} $p < .01$.^{***} $p < .0001$, tested against 0.

present for the baseline block ($F_{2,50} = .14$, $p = .87$, $\eta_p^2 = .01$), while, as predicted, the SCL during HL was significantly lower as compared to the Anxiety and Combined test blocks, which did not differ from each other ($F_{2,48} = 9.53$, $p < .01$, $\eta_p^2 = .28$; Load vs. Anxiety $t_{24} = -3.63$, $p < .01$; Load vs. Combined: $t_{24} = -3.79$, $p < .01$; Anxiety vs. Combined $t_{25} = -0.99$, $p = .33$). Results of the control analysis on the tonic SCL values free of the phasic SCR confirmed the general pattern observed in the uncorrected data (Block \times Condition interaction $F_{2,48} = 7.27$, $p < .01$, $\eta_p^2 = .23$; no effect was present at Baseline: $F_{2,48} = .85$, $p = .43$, $\eta_p^2 = .03$; but the conditions were different at Test: $F_{2,48} = 7.98$, $p < .01$, $\eta_p^2 = .25$). Further analyses were also performed to explore the time course of this effect, by dividing each block into two halves (first and second half, no overlap; see Fig. 3, main panel). Details concerning the results of these control analyses (which remained very consistent with the main analysis), and on the SCR analyses, can be found in the Supplementary Materials.

3.1.4. Affective response: stimuli ratings

The ratings of the eye stimuli were collected at the end of the experimental session, before it was ever mentioned to participants that the texture-like stimuli actually contained eyes (in fact, only 9 out of 28 participants mentioned something related to "eyes" when asked to report spontaneously what they saw in the periphery of the visual field during the main task). The ratings for valence showed

a trend towards an effect of stimulus type ($F_{2,50} = 2.78$, $p = .07$, $\eta_p^2 = .10$), whereby the lines stimuli were rated as being more positive ($M_{lines} = 4.1$, S.D. = 1.1) than the CE ($t_{25} = 2.2$, $p = .04$, $M_{CE} = 3.4$, S.D. = 1.5) and the FE ($t_{25} = 2.4$, $p = .03$, $M_{FE} = 3.4$, S.D. = 1.1), which did not differ from each other ($t_{25} = .09$, $p = .93$). Importantly, the arousal ratings of these stimuli clearly indicated an effect of stimulus type ($F_{2,50} = 16.15$, $p < .01$, $\eta_p^2 = .39$), whereby the lines stimuli were rated as being less arousing ($M_{lines} = 3.0$, S.D. = 1.4) than the CE ($t_{25} = 2.2$, $p = .04$, $M_{CE} = 3.8$, S.D. = 1.2) and the FE ($t_{25} = 5.9$, $p < .01$, $M_{FE} = 4.8$, S.D. = 1.2). Crucially, the FE were also rated as more arousing than the CE ($t_{25} = 3.7$, $p < .01$). Hence, we could conclude that these very simple texture stimuli somehow conveyed (albeit to a limited extent) a differential threatening content, expressed in their tendency to be recognized as more (FE) or less (CE) arousing. However, the lack of valence difference between control and fearful stimuli suggests that these simple textures were probably too simple to allow the full processing of their fear-related content.

3.2. ERP results: localizer

As expected given the main generator of this component in the calcarine fissure, a clear polarity reversal was evident for stimuli presented in the upper vs. lower visual field, with a distribution of this striate component at parieto-occipital leads (peak: 74 ms for UVF; 76 ms for LVF). All the three types of stimuli (Fearful Eyes, Con-

Table 2

Affective response.

	VAS baseline	VAS test	VAS difference	VAS _{pleas} baseline	VAS _{pleas} test	VAS _{tens} baseline	VAS _{tens} test
Load	46.1 (13.8)	52.6 (12.1)	6.5 mm ^{**}	50.6 (15.1)	43.7 (14.5)	42.9 (15.9)	49.0 (15.8)
Anxiety	45.8 (14.4)	55.7 (17.0)	9.8 mm [*]	50.4 (15.4)	43.3 (19.1)	42.8 (16.8)	54.7 (19.6)
Combined	48.0 (17.8)	58.3 (18.0)	10.2 mm ^{***}	47.4 (20.3)	40.0 (21.1)	43.5 (19.4)	56.5 (20.5)
	SCL baseline	SCL _{corr} baseline		SCL test		SCL _{corr} test	
Load	6.8 (2.6)				6.5 (2.8)		
Anxiety	6.7 (2.7)		6.7 (2.7)		7.0 (2.8)		6.9 (2.8)
Combined	6.9 (2.8)		6.9 (2.8)		7.1 (3.0)		7.1 (3.0)
	P300 baseline	P300 test		P300 difference			
Load	12.7 (5.0)	8.5 (5.9)		4.2 ^{**}			
Anxiety	13.8 (5.2)	12.2 (4.1)		1.6 [*]			
Combined	12.1 (4.9)	8.91 (5.1)		3.2 ^{**}			

Note. Upper panel: visual analogue scales (VAS, in mm) results for the compound score indicating distress (higher scores indicates higher distress) and the two separate scales for tension (VAS_{tens}) and pleasantness (VAS_{pleas}): for this scale, a higher score indicates a more pleasant state; pleasantness was reversed before pooling it with tension scores to obtain the overall VAS score). Although numerically the pure load condition increased distress the least, as compared to both conditions entailing the aversive sounds, none of the direct comparisons reached significance (load vs. threat $t_{25} = 1.43$, $p = .17$; load vs. combined: $t_{24} = 1.36$, $p = .19$). Middle panel: skin conductance levels (SCL, in μ S) at baseline and at test, for the three conditions. The SCL values for the conditions entailing threat sounds are presented raw (averaged over the full block duration) and corrected (SCL_{corr}), in order to compare SCL values that were unaffected by the phasic skin conductance responses to the aversive sounds (in the latter case). Therefore, SCL_{corr} values express the average of 5 time windows individually extracted for each participant in the 15 s preceding each sound (see methods). Lower panel: P300 amplitude measures (in μ V) for the three conditions and the two blocks.

^{*} $p < .05$.^{**} $p < .01$.^{***} $p < .0001$, tested against 0. SD values are expressed in parentheses.

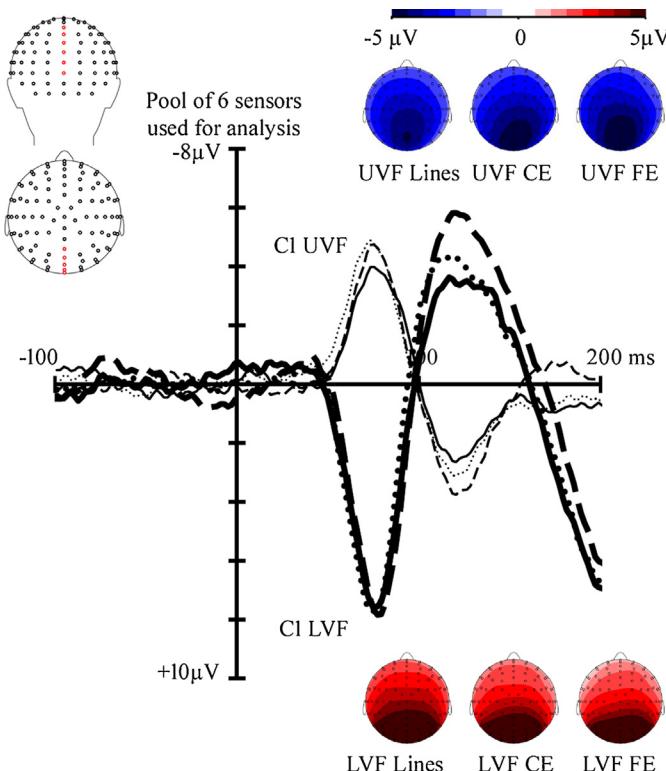


Fig. 4. Localizer.

Grand average ERP waveforms from the passive viewing localizer block, for Line stimuli (continuous lines), Control Eyes (CE, dashed lines) and fearful eyes (FE, dotted lines), shown separately for Upper Visual Field (UVF, thin lines) and Lower Visual Field. The plotted waveforms are obtained by pooling together the six channels used for C1 peak measurements and data analyses, as indicated in red in the blank maps on the left. In the insets, voltage maps for the three stimulus types presented in the UVF and LVF, at the peak of the C1 (74 ms for the UVF and 76 ms for the LVF) are provided.

trol Eyes and Lines) elicited a comparable C1 (see Fig. 4). The ANOVA on the C1 peak amplitude revealed only a significant main effect of Lead ($F_{5,125} = 9.99, p < .01, \eta_p^2 = .29$), but no effect of stimulus type ($F_{2,50} = 0.09, p = .92, \eta_p^2 = .003$), nor an interaction ($F_{10,250} = 1.02, p = .43, \eta_p^2 = .04$). This analysis on the independent localizer dataset confirmed that physical differences across the three type of peripheral textures did not per se cause any systematic variation in the C1 amplitude.

3.3. C1 during main task (see Fig. 5 and Supplementary Table III)

The ANOVA resulted in a main effect of Lead ($F_{5,110} = 14.02, p < .01, \eta_p^2 = .39$). The interaction between Condition and Block was significant ($F_{2,44} = 4.68, p = .01, \eta_p^2 = .18$), as well as the Condition \times Lead \times Block interaction ($F_{10,220} = 1.91, p = .04, \eta_p^2 = .08$), and, most importantly, the Condition \times Block \times Eye Type interaction ($F_{2,44} = 3.58, p = .04, \eta_p^2 = .14$). Given these interaction effects, we performed follow-up analyses of variance separately per Condition (with Lead, Block and Eye Type as factors), to test more formally which condition/manipulation (load alone, anxiety alone or their combination) led to an amplitude modulation of the C1, and in which direction.

3.3.1. Load condition

The ANOVA resulted in a main effect of Lead ($F_{5,110} = 9.67, p < .01, \eta_p^2 = .31$), indicating a similar scalp distribution in this condition as in the localizer, and a main effect of Block ($F_{1,22} = 6.62, p = .02, \eta_p^2 = .23$). Crucially, this main effect was further qualified by a significant interaction between Block and Eye Type ($F_{1,22} = 12.83,$

$p < .01, \eta_p^2 = .37$). This interaction was followed up by testing whether load effects were present on both stimulus types (cf. A right panel): results showed that while under HL the C1 for the Control eyes was significantly reduced in magnitude ($F_{1,22} = 25.14, p < .01, \eta_p^2 = .53$), by contrast, no effect of Load was present for the threat-related Fearful Eyes ($F_{1,22} = .03, p = .96, \eta_p^2 < .001$). These results clearly indicate that enhancing load at fixation increased the filtering of irrelevant information for the neutral stimuli (as it has been shown in the past for geometric figures, see Rossi & Pourtois 2012a, 2013), but that this effect was reduced (statistically absent) when the irrelevant information in the upper visual field contained material that was, because of its low level features, arousing and threat-related.

3.3.2. Anxiety condition

The ANOVA resulted in a main effect of Lead ($F_{5,110} = 14.76, p < .01, \eta_p^2 = .39$), and an interaction of Lead and Block ($F_{5,110} = 4.05, p = .01, \eta_p^2 = .16$). This interaction indicated that selectively during the Anxiety Block, the normal pattern of scalp distribution of the C1 component was slightly altered, being enhanced at dorsal scalp locations as compared to the safe condition (see Fig. 5B right panel). This might be taken as an indication that the brain response to all distractors was generally stronger in conditions of state anxiety as compared to a safe condition, without differences based on stimulus content.

3.3.3. Combined condition

The ANOVA on the combined condition resulted in a main effect of Lead ($F_{5,110} = 14.54, p < .01, \eta_p^2 = .34$). In addition, there was a significant interaction Lead \times Block \times Eye Type ($F_{5,110} = 3.40, p = .04, \eta_p^2 = .13$). This interaction was explained by a difference in the C1 amplitude (in favor of the FE, see Fig. 5C right panel) only at the most caudal Lead in the Test Block (HL + Anxiety, $t_{22} = 2.04, p = .05$), whereas in the baseline block the two stimuli elicited comparable C1 peaks. Note, crucially, that in conditions of enhanced state anxiety an increase in load, which should have caused filtering of irrelevant information, at least in the case of the neutral eyes, did not elicit any change at the level of the C1, as indicated by the absence of a main effect of Block ($F_{1,22} = 0.12, p = .73, \eta_p^2 = .005$) or an interaction Block \times Eye Type ($F_{1,22} = 1.09, p = .31, \eta_p^2 = .05$).

3.4. P300 in response to correctly identified targets (see Fig. 6 and Supplementary Table IV).

The ANOVA resulted in a main effect of Condition ($F_{2,50} = 8.31, p < .01, \eta_p^2 = .25$) and a main effect of Block ($F_{1,25} = 25.42, p < .01, \eta_p^2 = .50$), with no significant interaction effects (Block \times Condition: $F_{2,50} = 2.41, p = .10, \eta_p^2 = .09$). The main effect of Condition was explained by an overall higher P300 amplitude for the Anxiety Condition as compared to the two conditions entailing increased Load (see A–C). More interestingly, the P300 amplitude for targets was reduced in the Test Blocks, as compared to Baseline (for descriptive statistics, see Table 2), indicating a generalized impaired target processing when load was high, as well as during anxiety.

4. Discussion

In this study, we used a multi-measure approach to explore effects of state anxiety on electrophysiological indices reflecting cognitive biases. These were defined in two ways: first, an attentional bias for threat was quantified as an early sensory preference (enhanced ERP amplitude at the C1 level, ~75 ms after stimulus onset) for threat-related, as compared to neutral, stimuli presented at an unattended location (i.e., periphery of the upper visual field). The second type of bias that we focused on was related to the

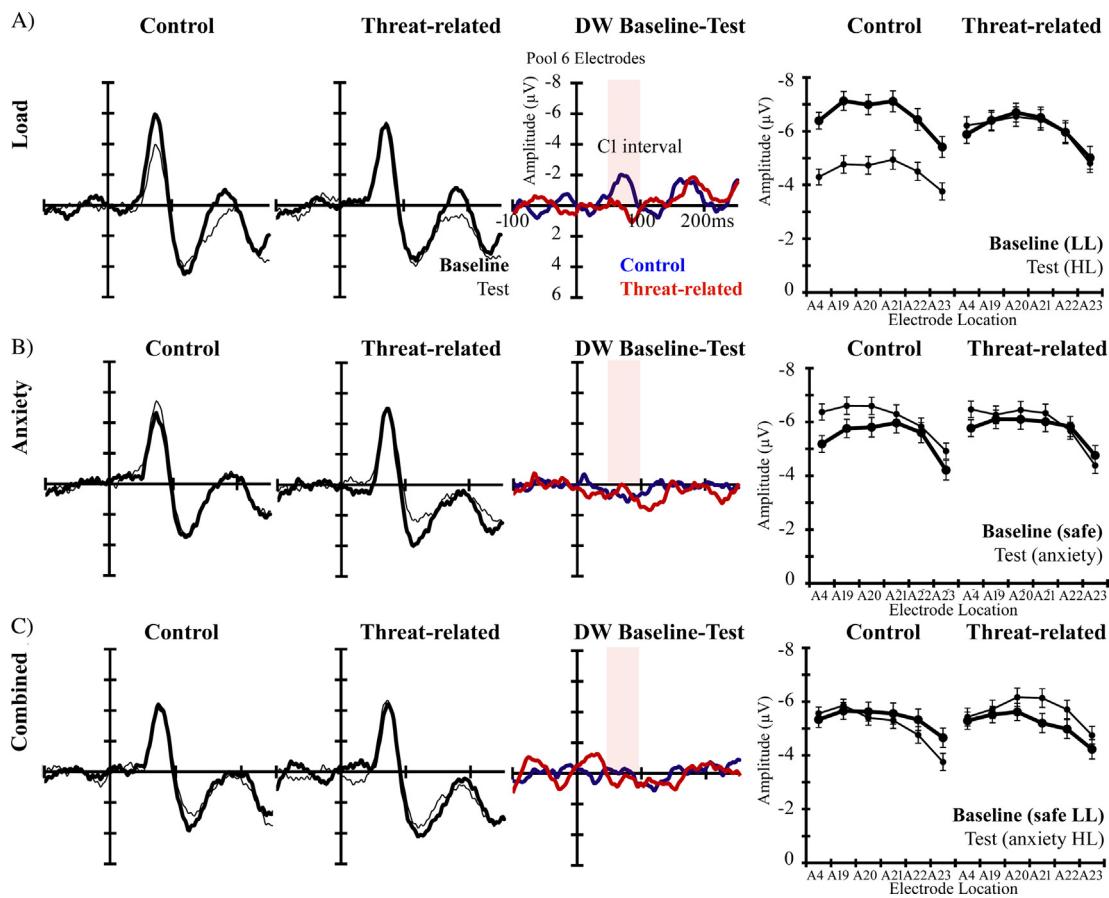


Fig. 5. Visual Evoked Potentials for peripheral stimuli during the main task. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(A) Load condition (B) Anxiety condition (C) Combined condition. ERP waveforms averaged across 6 electrodes used for C1 data analyses (A4/CPz, A19/Pz, A20/POz, A21/POz, A22/POOz, A23/Oz), for baseline block (thick lines) and test block (thin lines), separately for the Control stimuli (leftmost column) and the threat-related stimuli (second column). In the third column, the difference waveforms (DW) obtained by subtracting the ERPs for the test blocks from the ERPs in the baseline blocks, for the Control (blue) and the Threat-related stimuli (red) are provided. In the rightmost column, the line graphs represent the significant effects resulting from the statistical analyses: interaction between Block and Stimulus type in the Load condition (A); interaction between Lead and Block in the Anxiety condition (B); interaction between Lead, Stimulus type and Block in the combined condition, with a significantly higher C1 for threat-related stimuli selectively at A23 (most caudal lead) during the Test block (HL + anxiety). Of note the absence of a load effect for the control stimuli during the combined condition. Error bars represent 1 SEM.

balance between goal-driven processing and involuntary attentional capture: regardless of stimulus content, we tested whether state anxiety would interfere with top-down attention allocation (resulting in a decreased target-P300 amplitude) in favor of a more sensory-driven processing style (augmented C1 amplitude), when the stimuli themselves were kept identical across conditions. An overview of our different results can be found in Table 3. Moreover, we tested the hypothesis that the engagement in a HL task could perhaps diminish the anxious response to the state anxiety induction. Based on a push-pull mechanism regulating the distribution of resources between “emotional” processing and “cold”

cognition (Drevets & Raichle 1998), high load tasks have previously been used to reduce affective responses to emotional stimuli, de facto attenuating anticipatory anxiety (Kalisch, Wiech, Critchley, & Dolan, 2006). Therefore, thanks to our multi-measure approach, we could test whether the effects of the anxiety induction would be lessened (at the subjective and psychophysiological levels) by adding a competing high-demand task (Van Dillen, Heslenfeld and Koole, 2009; Vytal et al., 2012).

We first ascertained that the elected state anxiety induction and load manipulation were efficient. As predicted, during the anxiety induction blocks participants reported increased subjective levels of distress, and showed enhanced bodily arousal (SCL). Noteworthy, this increased peripheral activation due to the unpredictable sound delivery (Schmitz & Grillon, 2012) was strong enough to last throughout the entire duration of these blocks, showing only mild habituation. Second, we verified that our load manipulation (in the absence of anxiety) produced the desired effects. As expected, participants made more errors and were slower in detecting HL targets, as compared to LL ones. Moreover, in line with previous ERP literature (e.g., Kim et al., 2008; Sawaki & Katayama 2007; Rossi & Pourtois 2012a, 2014; Verleger, Baur, Metzner, & Šmigasiewicz, 2014), correctly detected targets in the difficult (HL) condition elicited a smaller P300 response, as compared to easily detectable ones.

Table 3

Summary of main results obtained for each condition/strain: behavioral, psychophysiological and neurophysiological.

	Load Anxiety Combination (load + anxiety)		
Behavioral indices	—	—	—
Self-report distress	+	+	+
Peripheral arousal	—	+	+
Goal-relevant P300	—	—	—
Control peripheral stimuli C1	—	~	=
Threat-related peripheral stimuli C1 =	~	~	=

Note. “=” symbol indicates no change between baseline and test; “+” indicates an increase; “—” indicates a decrease; “~” indicates the absence of a specific effect, but a general (main effect) trend towards an increase.

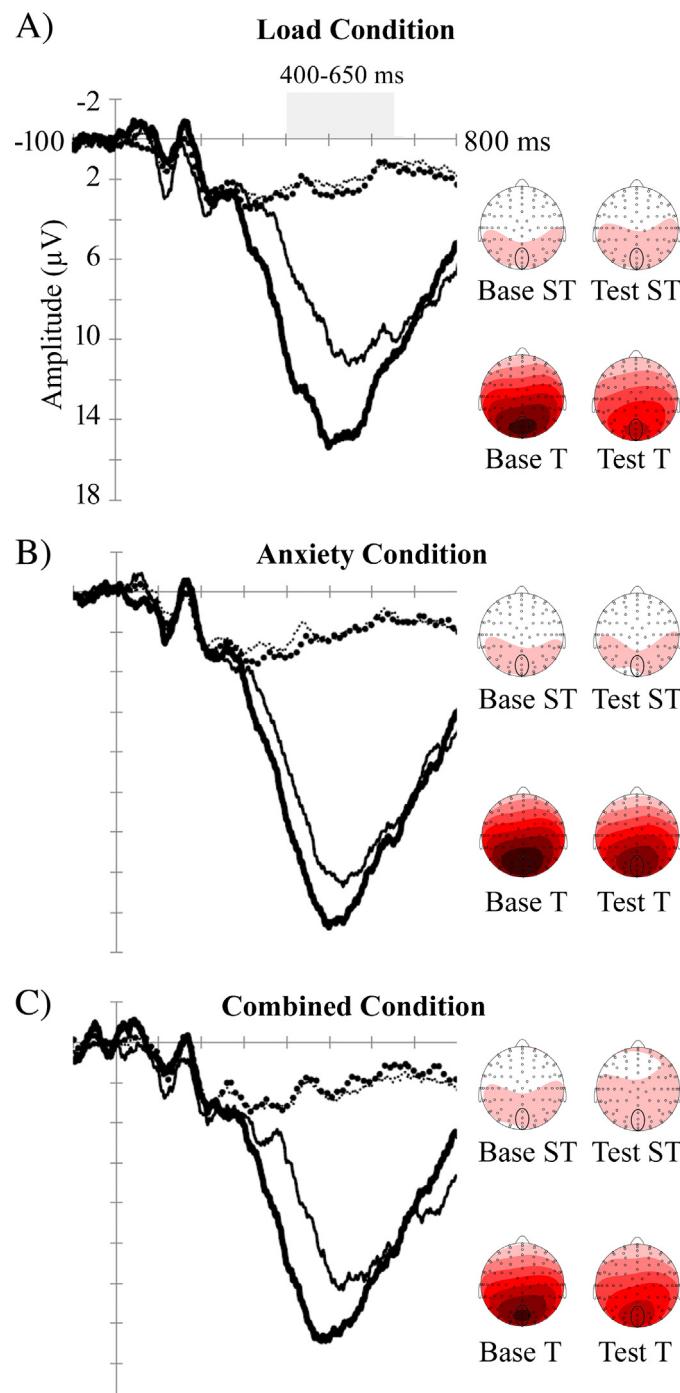


Fig. 6. ERPs for goal-relevant stimuli.

(A) Load condition (B) Anxiety condition C) Combined condition. ERP waveforms averaged across 4 electrodes used for P300 data analyses (A4/CPz, A19/Pz, A20/PPOz, A21/POz, highlighted in the map view), for standard stimuli (dotted lines) and target stimuli (full lines). Thick lines represent ERP responses during the baseline blocks, while thin lines depict ERP responses during test blocks, for the three conditions/strains separately (Load, Anxiety, and Combination). The topographical maps (top view) depict the voltage distribution on scalp during the interval used for ERP analyses (400–650 ms), separately for standard stimuli (ST) and target stimuli (T), for Baseline (Base) and Test blocks.

4.1. Sensory bias for threat in early visual areas

In our study, the threat-related stimulus consisted of a high-contrast texture composed of human fearful eye whites, which were chosen because of their preponderant role in fear detection (Ahs et al., 2014; Hardee, Thompson, & Puce, 2008; Schyns et al., 2007), as well as their preferential processing by the amygdala (Whalen et al., 2004). Given the tight and reciprocal anatomi-

cal connections between the amygdala and the occipital cortex, including V1 (Amaral, Behniea, & Kelly, 2003; Pourtois, Schettino, & Vuilleumier, 2013; Vuilleumier, 2005), and given that the intensity of responses in the amygdala has been shown to correlate, in fearful individuals, with the responses in visual cortex (for fear cues: Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005), we expected to observe stronger early visual responses at the C1 level to these fearful stimuli as compared to the control condition (neutral eye

whites), prior to any state anxiety induction or perceptual load increase. However, although post-experiment ratings confirmed that these fearful eye-whites were judged as negative, and more arousing than the neutral eye-whites, we did not observe any significant difference at the C1 level between these two stimulus types. Several reasons may potentially explain this lack of differentiation.

First, it could be that the preference for these fearful eye stimuli, that is commonly observed in limbic areas (such as the amygdala, Scheller, Büchel, & Gamer, 2012; Whalen et al., 2004), cannot be detected at the level of primary visual cortex at such an early latency following stimulus onset. However, two earlier ERP studies already reported increased C1 amplitudes for fearful as compared to scrambled, neutral and happy faces, in the absence of any concurrent state manipulation (Pourtois et al., 2004; West et al., 2011), suggesting that this early ERP component is not blind to stimulus-related emotional effects. In addition, two previous ERP studies used classical conditioning (gratings; Hintze et al., 2014; Stolarova et al., 2006) and reported increased C1 amplitudes to negatively conditioned stimuli (CS+), confirming that this early visual component can very well capture changes in the (acquired) affective value of visual stimuli, with a preference (i.e., larger amplitude) for negative ones. Alternatively, we cannot exclude the possibility that these fearful eyes were simply not distinguished from neutral eyes early on following their onset in the primary visual cortex, and therefore no preference or negativity bias was visible in the C1 amplitude. However, a closer look at our new ERP results (see also Table 3) shows that when participants carried out a HL task, the C1 component in response to the fearful stimuli was significantly increased as compared to the neutral ones, suggesting that the two types of stimuli were indeed differentiated rapidly following their onset. Moreover, when comparing directly LL and HL for the control stimuli, a very clear load effect was present (Rauss et al., 2009; Rossi & Pourtois 2012a, 2014), while for the fearful ones no early filtering was detectable, even under HL conditions. Therefore, our ERP findings suggest that a sensory bias for unattended threat-related stimuli can be measured as early as 75 ms after their onset, at least when perceptual load is increased. On the other hand, it is plausible that in the LL condition the detection task was too easy, so that a ceiling effect for the unattended stimuli shown in UVF overshadowed any possible bias for threat-related stimuli. As soon as a more demanding task was introduced, however, the attentional scope was narrowed, resulting in a reduced C1 for the control stimuli (Rossi & Pourtois, 2012a, 2014). Crucially, due to their intrinsic ability to attract attention in a partly automatic fashion (Okon-Singer, Tzelgov, Henik, 2007), the fearful displays were prioritized and resisted this filtering, capturing any spare attentional resources and eliciting unreduced responses in early visual areas. This account is in line with previous reports (e.g., Mothes-Lasch et al., 2013), in which enhanced fear processing was observed during a HL task, when the saliency of the eye area was high. By analogy with these earlier results, it is therefore likely that in our study, albeit task irrelevant, fearful eye-whites shown in the periphery gained saliency due to their abrupt onset, and therefore were preferentially processed in V1 rapidly following their onset during the HL blocks (for a review describing the constraints regulating emotional stimulus processing under different task demands, see Okon-Singer, Lichtenstein-Vidne and Cohen, 2013).

4.2. State anxiety and attentional capture: narrowing or hypervigilance?

Thus, we found evidence that under some constraints attention is preferentially allocated towards threat-related stimuli at the level of the C1. We could then assess effects of state anxiety on this early attentional bias for threat, and pit against each other two different accounts. On the one hand, state anxiety could

very well mimic the effects created by enhanced perceptual load on the attentional scope. In this framework, it would thus narrow the focus around fixation in the presence of neutral stimuli, as previously reported with a different type of anxiety induction (see Easterbrook, 1959; Rossi & Pourtois, 2012a, 2013, 2014). Alternatively, given the specifics of the anxiety induction used here (sharing some similarities with the use of noxious stimulations), one could argue that state anxiety would rather lead to sensory hypervigilance, thereby enhancing sensory responses to irrelevant information (Somerville et al., 2010). Our new ERP results clearly showed that the C1 to the peripheral stimuli (either neutral or threat-related) was not reduced when anxiety levels were enhanced; a finding which better fits the latter than the former framework, assuming that anxiety is related to hypersensitivity of the sensory system to salient information.

Usually, hypervigilance is conceived as a generic, stimulus-aspecific phenomenon, which is more related to an attentional set than to a specific stimulus category (Somerville et al., 2010, 2013). For example, amplitude variations in the C1 time window were reported in an earlier ERP study in a sample of spider fearful individuals, during a visual search task where the search arrays could (or not) contain a spider (Weymar et al., 2014). These authors reported a general increase of the C1 to all stimulus types in spider fearful individuals, and interpreted this finding as a generic hypervigilance phenomenon (thus not tagged to a specific stimulus type) triggered by the probable presence of spiders in this specific task context. On the other hand, another ERP study (Eldar, Yankelevitch, Lamy, & Bar-Haim, 2010) investigated early attentional biases for angry faces in trait anxious individuals in a dot-probe task. These authors reported increased C1 responses in high trait/state anxious participants selectively in trials containing angry faces, suggesting that the type of hypervigilance that might have mediated this effect was confined to threat cues (the angry faces), and did not generalize to neutral or happy stimuli. In the present study, state anxiety influenced the C1 amplitude in an undifferentiated fashion for both threat-related and neutral stimuli (cf. in Supplementary Table III the lack of a significant interaction between Block and Eye Type), suggesting that, in a threatening context, the early sensory response to irrelevant, abrupt stimuli is likely governed by a "task mode", rather than by the specific stimulus content. As such, our C1 results showing a generic anxiety-driven strengthening of early neural responses to peripheral stimuli, share similarities with the sensory hypervigilance observed in fearful individuals in a threatening context (Weymar et al., 2014).

As a matter of fact, the strongest evidence for the induction of a hypervigilant attentional state in our study came from the condition in which participants were asked to perform a HL task while enduring a heightened level of state anxiety (i.e., combined condition). Based on previous neuroimaging studies (see Rees et al., 1997; Rauss et al., 2009), as well as on the ERP results obtained for the "pure" load condition, one would *a priori* expect the C1 responses to the neutral stimuli to be strongly reduced in this condition, due to the high task demands imposing an early attentional bottleneck (see also Rossi & Pourtois, 2012a, 2014). However, our ERP results show instead that when state anxiety was added to the perceptual load manipulation, the C1 amplitude was not reduced as a function of task load anymore. In other words, in the race between enhanced top-down attention control (and in turn narrowing with increased load) and sensory hypervigilance (related to enhanced state anxiety), the latter may gain priority, and eventually impair the early attentional filters irrespective of the stimulus content (threat-related or not). These results reveal how state anxiety is a powerful factor biasing the way attention resources are distributed to effectively deal with changing environmental con-

tingencies, and highlight how this redistribution of resources might become inefficient at times (Bishop, 2009).

4.3. State anxiety and attentional redistribution: effects on goal-directed processing

Noteworthy, our study also highlights how this early sensory prioritization of irrelevant information, during the experience of increased arousal and distress, leads to deteriorated goal-directed processing, in line with models proposing a constant struggle for balance between the “emotional” and the “cognitive” brain, with context-dependent effects on attention control (Okon-Singer, Handler, Pessoa, & Shackman, 2015). Although during the pure anxiety condition task demands were kept low in perceptual load, participants’ detection performance was significantly impaired, both in RT and accuracy. At the electrophysiological level, in line with several previous ERP studies (Moser et al., 2005; Rossi & Pourtois, 2014; Shackman et al., 2011), we found that state anxiety significantly reduced the target P300 despite the use of an “easy” discrimination task. Accordingly, our new P300 results are in line with the prediction that goal-directed processing, reflected by this post-perceptual ERP component, became more cumbersome when participants were exposed to an aversive stimulus that they could neither predict nor avoid, possibly due to an imbalance in favor of bottom-up attentional capture (as reflected by the generic hypervigilance measured at the C1 level in our ERP results). These effects might be tentatively attributed to diminished resource availability within the fronto-parietal attentional networks, particularly in the right hemisphere (Rossi & Pourtois, 2014; Shackman et al., 2006).

Interestingly, in contrast with models implicating processing efficiency costs in anxiety (and thus predicting increased anxiety costs in more demanding conditions, while easier task should be relatively spared; see Eysenck, Derakshan, Santos, & Calvo, 2007), anxiety interfered with performance mostly in the LL blocks, while in the combined condition neither RTs nor accuracy were further impaired, relative to the HL (and no anxiety) condition. These results, confirmed by our P300 findings, resemble earlier neuroimaging findings showing that low and high anxious participants performed equally well in HL tasks (where the need for recruiting prefrontal attentional control is kept constant), but not in LL tasks (where this recruitment is intermittent, and trait anxiety impaired performance; see Bishop, 2009). Moreover, they confirm predictions drawn by behavioral studies showing how in difficult conditions (HL, incongruent trials) the effects of anxiety become negligible, while they are destructive in case of lower task demands (Hu et al., 2012; Vytal et al., 2012).

Notwithstanding these findings, we failed to evidence a “protective” effect of task load on anxious response, both at the subjective and at the peripheral arousal level (see Table 3). Comparing pure state anxiety induction to the combination of state anxiety and enhanced perceptual load shows that the anxious response at the psychophysiological level developed equally strongly in both cases, in contrast with our predictions. Although based on previous literature we would expect a milder effect of the induction protocol while participants were engaged in a difficult task, we can interpret this result based on recent psychophysiological studies, showing that such an implicit emotion regulation is actually the most effective when the concurrent task is of verbal nature (Vytal et al., 2012). Given that in the present case the task at hand was visual and perceptual in essence, it did not shield participants against the experience of negative affect. Moreover, our anxiety inducing stimuli were unpredictable and very salient, and therefore difficult to suppress (which might very well have contributed to the creation of the hypervigilant state in the first place).

5. Conclusions

Using a task that varied in perceptual load, performed during either a neutral or an anxious state, we could show that a perceptual bias for threat-related stimuli could be observed rapidly following stimulus onset at the level of the C1, as long as the perceptual load of the task at hand was kept high. Hence, these results show that early sensory processing (captured by the C1 component) can be the locus of short term plasticity, in the sense that salient events (here threat-related stimuli) readily receive prioritization when needed. Importantly, our new results also show that this early sensory prioritization of salient stimuli is accompanied by a cost for goal-directed processing, which can be evidenced both at the behavioral and electrophysiological levels. Moreover, when a HL task needs to be performed during a heightened state of anxiety, the additional (top-down) control required to maintain performance can be achieved, while it is partially disrupted when the load is low, and control has to be recruited in a phasic fashion. However, in this situation where two strains (load and anxiety) directly compete for attention selection, we found evidence for a state of sensory hypervigilance, as translated in an impaired early filtering of irrelevant information (which would be adaptive to maintain performance in case the distractors would happen to be incompatible with the desired response). Hence, state anxiety appears to create a perceptual bias towards the rapid processing of external stimuli, at the expense of goal-directed top-down processing. Whether or not similar (or even exacerbated) imbalances or asymmetries between top-down and bottom-up processes during attention selection could also be observed when anxiety becomes chronic and stable awaits empirical validation.

Acknowledgements

This work was supported by a grant from the European Research Council (Starting Grant #200758 to GP), by the Special Research Funds at Ghent University (BOF Grant #05Z01708 to GP and #BOF13/PDO/095 to VR) and by the Belgian Science Policy, Interuniversity Attraction Poles program (P7/11).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biopsycho.2015.10.014>.

References

- Ahs, F., Davis, C. F., Gorka, A. X., & Hariri, A. R. (2014). Feature-based representations of emotional facial expressions in the human amygdala. *Social Cognitive and Affective Neuroscience*, 9(9), 1372–1378.
- Amaral, D. G., Behnia, H., & Kelly, J. L. (2003). Topographic organization of projections from the amygdala to the visual cortex in the macaque monkey. *Neuroscience*, 118(4), 1099–1120.
- Amodio, D. M., Bartholow, B. D., & Ito, T. A. (2014). Tracking the dynamics of the social brain: ERP approaches for social cognitive and affective neuroscience. *Social Cognitive and Affective Neuroscience*, 9(3), 385–393.
- Bishop, S. J. (2009). Trait anxiety and impoverished prefrontal control of attention. *Nature Neuroscience*, 12(1), 92–98.
- Bishop, S. J., Jenkins, R., & Lawrence, A. D. (2007). Neural processing of fearful faces: effects of anxiety are gated by perceptual capacity limitations. *Cerebral Cortex*, 17(7), 1595–1603.
- Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: the BIS/BAS scales. *Journal of Personality and Social Psychology*, 67(2), 319–333.
- Cornwell, B. R., Alvarez, R. P., Lissek, S., Kaplan, R., Ernst, M., & Grillon, C. (2011). Anxiety overrides the blocking effects of high perceptual load on amygdala reactivity to threat-related distractors. *Neuropsychologia*, 49(5), 1363–1368.
- Drevets, W. C., & Raichle, M. E. (1998). Suppression of regional cerebral blood during emotional versus higher cognitive processes: implications for interactions between emotion and cognition. *Cognition and Emotion*, 12, 353–385.

- Dvorak-Bertsch, J. D., Curtin, J. J., Rubinstein, T. J., & Newman, J. P. (2007). Anxiety moderates the interplay between cognitive and affective processing. *Psychological Science*, 18(8), 699–705.
- Easterbrook, J. A. (1959). The effect of emotion on cue utilization and the organization of behavior. *Psychological Review*, 66(3), 183–201.
- Eldar, S., Yankelevitch, R., Lamy, D., & Bar-Haim, Y. (2010). Enhanced neural reactivity and selective attention to threat in anxiety. *Biological Psychology*, 85(2), 252–257.
- Everaert, T., Spruyt, A., Rossi, V., Pourtois, G., & De Houwer, J. (2013). Feature-specific attention allocation overrules the orienting response to emotional stimuli. *Social Cognitive and Affective Neuroscience*.
- Eysenck, M. W., Derakshan, N., Santos, R., & Calvo, M. G. (2007). Anxiety and cognitive performance: attentional control theory. *Emotion*, 7(2), 336–353.
- Foxe, J. J., & Simpson, G. V. (2002). Flow of activation from V1 to frontal cortex in humans—a framework for defining early visual processing. *Experimental Brain Research*, 142(1), 139–150.
- Fu, S., Fedota, J. R., Greenwood, P. M., & Parasuraman, R. (2012). Dissociation of visual C1 and P1 components as a function of attentional load: an event-related potential study. *Biological Psychology*, 85(1), 171–178.
- Gratton, G., Coles, M. C., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55(4), 468–484.
- Hardee, J. E., Thompson, J. C., & Puce, A. (2008). The left amygdala knows fear: laterality in the amygdala response to fearful eyes. *Social Cognitive and Affective Neuroscience*, 3(1), 47–54.
- Hintze, P., Junghofer, M., & Bruchmann, M. (2014). Evidence for rapid prefrontal emotional evaluation from visual evoked responses to conditioned gratings. *Biological Psychology*, 99, 125–136.
- Hu, K., Bauer, A., Padmala, S., & Pessoa, L. (2012). Threat of bodily harm has opposing effects on cognition. *Emotion (Washington, D.C.)*, 12(1), 28–32.
- Jeffreys, D. A., & Axford, J. G. (1972). Source locations of pattern-specific components of human visual evoked-potentials. I. Component of striate cortical origin. *Experimental Brain Research*, 16(1), 1–21.
- Kalisch, R., Wiech, K., Critchley, H. D., & Dolan, R. J. (2006). Levels of appraisal: a medial prefrontal role in high-level appraisal of emotional material. *NeuroImage*, 30(4), 1458–1466.
- Keil, A., Debener, S., Gratton, G., Junghofer, M., Kappenman, E. S., Luck, S. J., et al. (2014). Committee report: publication guidelines and recommendations for studies using electroencephalography and magnetoencephalography. *Psychophysiology*, 51(1), 1–21.
- Kim, K. H., Kim, J. H., Yoon, J., & Jung, K.-Y. (2008). Influence of task difficulty on the features of event-related potential during visual oddball task. *Neuroscience Letters*, 445(2), 179–183.
- Lavie, N. (2005). Distracted and confused? Selective attention under load. *Trends in Cognitive Sciences*, 9(2), 75–82.
- Moser, J. S., Hajcak, G., & Simons, R. F. (2005). The effects of fear on performance monitoring and attentional allocation. *Psychophysiology*, 42(3), 261–268.
- Mothes-Lasch, M., Mentzel, H.-J., Miltner, W. H. R., & Straube, T. (2013). Amygdala activation to fearful faces under attentional load. *Behavioural Brain Research*, 237(0), 172–175.
- Nolen-Hoeksema, S., & Morrow, J. (1991). A prospective study of depression and posttraumatic stress symptoms after a natural disaster: the 1989 Loma Prieta Earthquake. *Journal of Personality and Social Psychology*, 61(1), 115–121.
- Okon-Singer, H., Hendler, T., Pessoa, L., & Shackman, A. J. (2015). The neurobiology of emotion-cognition interactions: fundamental questions and strategies for future research. *Frontiers in Human Neuroscience*, 9, 58.
- Okon-Singer, H., Lichtenstein-Vidne, L., & Cohen, N. (2013). Dynamic modulation of emotional processing. *Biological Psychology*, 92(3), 480–491.
- Okon-Singer, H., Tzelgov, J., & Henik, A. (2007). Distinguishing between automaticity and attention in the processing of emotionally significant stimuli. *Emotion*, 7(1), 147–157.
- Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proceedings of the National Academy of Sciences of the United States of America*, 99(17), 11458–11463.
- Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, 14(6), 619–633.
- Pourtois, G., Schettino, A., & Vuilleumier, P. (2013). Brain mechanisms for emotional influences on perception and attention: what is magic and what is not. *Biological Psychology*, 92(3), 492–512.
- Rauss, K., Pourtois, G., Vuilleumier, P., & Schwartz, S. (2009). Attentional load modifies early activity in human primary visual cortex. *Human Brain Mapping*, 30(5), 1723–1733.
- Rauss, K., Schwartz, S., & Pourtois, G. (2011). Top-down effects on early visual processing in humans: a predictive coding framework. *Neuroscience & Biobehavioral Reviews*, 35(5), 1237–1253.
- Rauss, K., Pourtois, G., Vuilleumier, P., & Schwartz, S. (2012). Effects of attentional load on early visual processing depend on stimulus timing. *Human Brain Mapping*, 33, 63–74.
- Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science*, 278(5343), 1616–1619.
- Robinson, O. J., Vytal, K., Cornwell, B. R., & Grillon, C. (2013). The impact of anxiety upon cognition: perspectives from human threat of shock studies. *Frontiers in Human Neuroscience*, 7.
- Rossi, V., & Pourtois, G. (2012a). State-dependent attention modulation of human primary visual cortex: a high density ERP study. *Neuroimage*, 60(4), 2365–2378.
- Rossi, V., & Pourtois, G. (2012b). Transient state-dependent fluctuations in anxiety measured using STAI, POMS, PANAS or VAS: a comparative review. *Anxiety, Stress and Coping*, 25(6), 603–645.
- Rossi, V., & Pourtois, G. (2013). Negative affective state mimics effects of perceptual load on spatial perception. *Emotion*, 13(3), 485–496.
- Rossi, V., & Pourtois, G. (2014). Electrical neuroimaging reveals content-specific effects of threat in primary visual cortex and fronto-parietal attentional networks. *NeuroImage*, 98, 11–22.
- Sabatinelli, D., Bradley, M. M., Fitzsimmons, J. R., & Lang, P. J. (2005). Parallel amygdala and inferotemporal activation reflect emotional intensity and fear relevance. *NeuroImage*, 24(4), 1265–1270.
- Sawaki, R., & Katayama, J. (2007). Difficulty of discrimination modulates attentional capture for deviant information. *Psychophysiology*, 44(3), 374–382.
- Scheller, E., Büchel, C., & Gamer, M. (2012). Diagnostic features of emotional expressions are processed preferentially. *PLoS One*, 7(7), e41792.
- Schmitz, A., & Grillon, C. (2012). Assessing fear and anxiety in humans using the threat of predictable and unpredictable aversive events (the NPU-threat test). *Nature Protocols*, 7(3), 527–532.
- Schupp, H. T., Öhman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: an ERP analysis. *Emotion*, 4, 189–200.
- Schwartz, S., Vuilleumier, P., Hutton, C., Maravita, A., Dolan, R. J., & Driver, J. (2005). Attentional load and sensory competition in human vision: modulation of fMRI responses by load at fixation during task-irrelevant stimulation in the peripheral visual field. *Cerebral Cortex*, 15(6), 770–786.
- Schyns, P. G., Petro, L. S., & Smith, M. L. (2007). Dynamics of visual information integration in the brain for categorizing facial expressions. *Current Biology*, 17(18), 1580–1585.
- Shackman, A. J., Maxwell, J. S., McMenamin, B. W., Greischar, L. L., & Davidson, R. J. (2011). Stress potentiates early and attenuates late stages of visual processing. *The Journal of Neuroscience*, 31(3), 1156–1161.
- Shackman, A. J., Sarinopoulos, I., Maxwell, J. S., Pizzagalli, D. A., Lavric, A., & Davidson, R. J. (2006). Anxiety selectively disrupts visuospatial working memory. *Emotion*, 6, 40–61.
- Somerville, L. H., Wagner, D. D., Wig, G. S., Moran, J. M., Whalen, P. J., & Kelley, W. M. (2013). Interactions between transient and sustained neural signals support the generation and regulation of anxious emotion. *Cerebral Cortex*, 23(1), 49–60.
- Somerville, L. H., Whalen, P. J., & Kelley, W. M. (2010). Human bed nucleus of the stria terminalis indexes hypervigilant threat monitoring. *Biological Psychiatry*, 68(5), 416–424.
- Spielberger, C. D. (1983). *Manual for the state-trait anxiety inventory (form Y) self-evaluation questionnaire*. Palo Alto, CA: Consulting Psychologists Press.
- Stolarova, M., Keil, A., & Moratti, S. (2006). Modulation of the C1 visual event-related component by conditioned stimuli: evidence for sensory plasticity in early affective perception. *Cerebral Cortex*, 16(6), 876–887.
- Van Dillen, L. F., Heslenfeld, D. J., & Koole, S. L. (2009). Tuning down the emotional brain: an fMRI study of the effects of cognitive load on the processing of affective images. *NeuroImage*, 45(4), 1212–1219.
- Vanlessen, N., Rossi, V., Raedt, R., & Pourtois, G. (2013). Positive emotion broadens attention focus through decreased position-specific spatial encoding in early visual cortex: evidence from ERPs. *Cognitive, Affective, & Behavioral Neuroscience*, 13(1), 60–79.
- Vanlessen, N., Rossi, V., Raedt, R., & Pourtois, G. (2014). Feeling happy enhances early spatial encoding of peripheral information automatically: electrophysiological time-course and neural sources. *Cognitive, Affective, & Behavioral Neuroscience*, 14(3), 951–969.
- Verleger, R., Baur, N., Metzner, M. F., & Śmigasiewicz, K. (2014). The hard oddball: effects of difficult response selection on stimulus-related P3 and on response-related negative potentials. *Psychophysiology*, 51(11), 1089–1100.
- Vuilleumier, P. (2005). How brains beware: neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, 9(12), 585–594.
- Vuilleumier, P. (2015). Affective and motivational control of vision. *Current Opinion in Neurology*, 28(1), 29–35.
- Vytal, K., Cornwell, B., Arkin, N., & Grillon, C. (2012). Describing the interplay between anxiety and cognition: from impaired performance under low cognitive load to reduced anxiety under high load. *Psychophysiology*, 49(6), 842–852.
- West, G. L., Anderson, A. A. K., Ferber, S., & Pratt, J. (2011). Electrophysiological evidence for biased competition in V1 for fear expressions. *Journal of Cognitive Neuroscience*, 1–10.
- Weymar, M., Keil, A., & Hamm, A. O. (2014). Timing the fearful brain: unspecific hypervigilance and spatial attention in early visual perception. *Social Cognitive and Affective Neuroscience*, 9(5), 723–729.
- Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., et al. (2004). Human amygdala responsivity to masked fearful eye whites. *Science*, 306(5704), 2061.