

Negative Affective State Mimics Effects of Perceptual Load on Spatial Perception

Valentina Rossi and Gilles Pourtois
Ghent University

Recent electrophysiological evidence has shown that perceptual load and negative affective state can produce very similar, early-attention gating effects in early visual areas, modulating the processing of peripheral stimuli. Here we assessed the question of whether or not these modulatory effects of perceptual load and negative affect (NA) lead to comparable changes in spatial perception abilities, which could be captured at the behavioral level. High perceptual load at fixation impaired the precise spatial localization of peripheral textures, relative to a low perceptual load condition. By contrast, the coarse spatial encoding of these peripheral stimuli was not load-dependent, under neutral affective conditions. The transient experience of NA was induced in an independent sample of participants, who showed decreased performance in the localization task, even at a low perceptual-load level. These results were observed in the absence of any systematic eye movement toward the peripheral textures. These findings suggest that spatial location perception is an attention-dependent, as well as state-dependent process, in the sense that NA, very much like load, can dynamically shape early spatial perceptual abilities. Although NA mimics load during spatial localization, we discuss the possibility that these two effects likely depend upon nonoverlapping brain networks.

Keywords: attention, anxiety, spatial perception, spatial resolution, rumination

The hybrid theory of selective attention postulates that full resource allocation is a dynamic and automatic process (Lavie, 1995; Lavie & Tsai, 1994). Neuroimaging and electrophysiological studies have provided converging evidence for this assumption, showing that the strength of neural responses to (unattended) stimuli shown in the peripheral visual field actually depends upon the amount of residual attentional capacity left over by the primary task (e.g., Rauss, Pourtois, Vuilleumier, & Schwartz, 2009; Rees, Frith & Lavie, 1997; Schwartz, Vuilleumier, Hutton, Maravita, Dolan, & Driver, 2005).

These effects are typically considered to be structural, therefore state-invariant. However, enhanced levels of NA have been shown to influence memory for (Wessel & Merckelbach, 1997), or selective attention to peripheral stimuli (Chajut & Algom, 2003; Fenske & Eastwood, 2003; Finucane & Power, 2010), therefore suggesting that the spillover of attention to irrelevant stimuli might not be invariable, but instead flexibly modulated by situational factors (e.g., affective state). In line with this view, Schmitz and colleagues (Schmitz, De Rosa, & Anderson, 2009) showed that the size of the attentional focus could be modulated, depending on the

current affective state of the participant. In a functional neuroimaging study, they demonstrated that induced negative mood narrowed this focus (operationalized as the amplitude of extrastriate visual cortex response to specific parafoveal stimuli), whereas more positive moods broadened it. Of interest, the authors suggested that these state-dependent affect-driven differences taking place in extrastriate visual cortical areas were not ascribed to (distant) changes in top-down, frontal attentional control mechanisms (Corbetta & Shulman, 2002), but instead to qualitative changes in stimulus encoding in earlier visual areas. In line with the brain-imaging evidence and the interpretation put forward by Schmitz and colleagues, in a recent event-related brain potential (ERP) study, we showed that affective states reliably influenced the earliest sweep of cortical activation in response to irrelevant, neutral peripheral stimuli (Rossi & Pourtois, 2012). This early cortical response was quantified as the amplitude of the C1 (Clark, Fan, & Hillyard, 1994; Foxe & Simpson, 2002; Rauss, Schwartz, & Pourtois, 2011), an ERP component classically ascribed to activations in the fundus of the calcarine cortex. In detail, we observed that this component, primarily sensitive to the position of the stimulus in the visual field (Jeffreys & Axford, 1972), but also sensitive to perceptual load manipulations (Rauss et al., 2009, 2011), was strongly reduced in amplitude when participants underwent an NA induction. In other words, during the experience of the NA state, the earliest visual response to peripheral stimuli was suppressed as much as during high perceptual load.

Besides showing that load effects were not only depending on structural factors, these results stimulated the question of whether the two types of effects (load-dependent vs. affective state-dependent), producing similar changes early on following stimulus onset at the electrophysiological level, could also be traced at the behavioral level. Given the tight link between the C1 ERP com-

This article was published Online First December 3, 2012.

Valentina Rossi and Gilles Pourtois, Psychopathology and Affective Neuroscience Laboratory, Department of Experimental-Clinical and Health Psychology, Ghent University, Ghent, Belgium.

This work was supported by a grant from the European Research Council (Starting Grant #200758).

Correspondence concerning this article should be addressed to Valentina Rossi, Department of Experimental-Clinical and Health Psychology, Ghent University, Henri Dunantlaan 2, 9000 Ghent, Belgium. E-mail: Valentina.Rossi@UGent.be

ponent and an early retinotopic encoding of visual stimuli, we suggested that perceptual load and NA would primarily impair the ability to localize in space peripheral stimuli (as opposed to reducing the detection of their content, e.g.). However, in earlier ERP and neuroimaging studies (Rauss et al., 2009, 2011; Rossi & Pourtois, 2012; Schmitz et al., 2009), as well as in most of the literature lending support to the load theory (cf., Lavie, 2005, for a review), the processing of the peripheral stimuli remained usually implicit, and therefore the issue of whether or not their spatial perception was actually affected by load or affect was not directly addressed. However, independent evidence in the literature suggests that perceptual load can impair the perception of onsets of peripheral stimuli (e.g., Macdonald & Lavie, 2008). Based on these behavioral findings, and in light of our previous neurophysiological studies showing that perceptual load and NA alike disrupt early retinotopic responses to peripheral visual stimuli (Rauss et al., 2009; Rossi & Pourtois, 2012), we focused on two specific questions in this study: Does an increased perceptual load (at fixation) impair localization abilities for peripheral stimuli? Furthermore, and crucially, is the transient induction of NA sufficient to cause a load-like effect on the spatial localization of these same peripheral stimuli? To address these questions we asked participants to estimate the spatial localization of peripherally presented textures, while they performed either an easy or a more difficult task at fixation, creating two levels of perceptual load. Half of the participants were tested in neutral conditions (i.e., no affective manipulations), and the other half underwent a validated NA induction procedure based on the use of bogus negative feedbacks on one's own task performance (Rossi & Pourtois, 2012). First, we tested the prediction that increasing perceptual load at fixation would alter the ability to determine the exact spatial localization of the peripheral stimuli, in agreement with our previous ERP results. Following coarse coding models of perception, fine spatial localization is improved for stimuli shown in portions of the visual field that are covertly attended to by participants; coarse coding can be performed preattentively (Newby & Rock, 2001; Prinzmetal, Amiri, Allen, & Edwards, 1998; Tsal & Bareket, 1999, 2005). Accordingly, we expected the capacity to coarsely localize stimuli in peripheral space to be preserved even under high load, whereas load-dependent inattention would decrease precision as well as increase response shifts (Chastain, 1986), as compared with the low-load condition. Furthermore, based on our previous ERP findings, which showed that load-dependent modulatory effects influencing early visual cortex were basically abolished when participants experienced enhanced levels of NA (Rossi & Pourtois, 2012), we also surmised that the transient experience of NA could mimic the effects of perceptual load, namely, reduce the precise spatial localization of the peripheral stimuli even under low load.

Even though we predict similar effects of load and NA on spatial localization abilities, we believe that these two effects might very well stem from different brain circuits. In detail, whereas NA state-dependent effects might arise from the selective engagement of ventral (i.e., amygdala-prefrontal) emotion-control systems that eventually exert load-like modulatory effects in the visual cortex (Pourtois, Schettino, & Vuilleumier, 2012), dorsal (fronto-parietal) attention-control networks are assumed to play a critical role during load (Pessoa & Adolphs, 2010).

Method

Participants

One hundred and one right-handed undergraduate students took part in this experiment in exchange for course credits. Participants had normal or corrected-to-normal vision, and were unaware of the purpose of the study. The data of four participants, who admitted during the debriefing not to have carried out the secondary task, were excluded from the analyses, resulting in a final sample of 97 participants ($M_{\text{age}} = 20.4$ years, $SD = 3.4$ years, 12 males). Participants received the task either under neutral conditions (neutral group, $N = 48$) or after undergoing an NA/state-anxiety induction (NA group, $N = 49$). In this latter group, eye movements were also recorded online during the main task (and directly compared with a control condition in which volitional saccadic eye movements were required), using an oculogram. Due to technical problems, the recording of eye movements could not be completed properly in two participants. Hence, all analyses of eye movements were based on a sample including 47 participants. The study protocol was designed and conducted in accordance with the Declaration of Helsinki (World Medical Association, 2008) and approved by the local ethics committee (Faculty of Psychology and Educational Sciences, Ghent University, Ghent, Belgium).

Stimuli and Apparatus

All participants were instructed to maintain fixation on a white cross presented against a black background in the center of a computer screen (19-in. CRT) throughout the experimental session. The cross subtended about a 0.5° visual angle. During the task, they received a rapid, serial visual presentation (RSVP) of tilted gray lines presented one at a time at fixation (see Figure 1). In each block, 80% of the line stimuli were identical (standards), and required no response. The standard lines were always equally tilted (35° clockwise in half of the session, counterclockwise in the other half of the session, subtending a 0.8° visual angle). Randomly intermixed with the standard lines, deviant lines with a different in-plane orientation were presented (20% of the trials); participants were instructed to treat them as targets, and respond to their presentation with a specific key press. The angular difference between standard and target stimuli was manipulated in order to obtain a binary variation along the perceptual load dimension (Rossi & Pourtois, 2012): In the low-load (LL) condition, the difference consisted in 10° of angle (that is, standards inclined 35° , targets inclined either 45° or 25°), whereas in the high-load condition (HL), it was reduced to 5° (standards inclined 35° , targets inclined either 40° or 30°). Target and standard lines were presented for 250 ms, with an average interstimulus interval (ISI) of 1325 ms (randomly varied between 1150 and 1500 ms). Peripheral, nonpredictive visual textures of horizontal line elements ($3^\circ \times 34^\circ$ of visual angle) were flashed for 250 ms in the upper visual field during the ISI, thus never overlapping in time with the presentation of the central stimuli. Earlier research identified two key aspects underlying spatial localization of peripheral stimuli: An azimuth or radial angle, and a distance from the center. The former component defines the position of the peripheral stimulus in relation to the center of the visual field (sets the "direction"), and it is relatively preserved even in unattended conditions (Tsal &

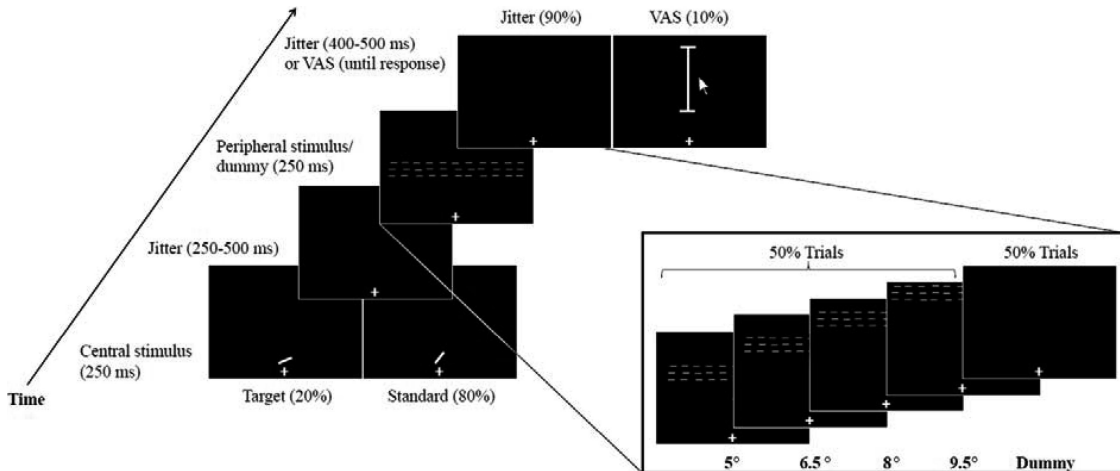


Figure 1. Trial structure. We used a modified version of the oddball detection task used in Rossi & Pourtois (2012). Standard or target line segments were presented using an RSVP at fixation. Only deviant target orientations required motor responses. In 50% of the trials, during the jittered interstimulus interval (ISI), a horizontal texture made of misaligned line elements was presented, at one of four possible locations. In 90% of the trials, participants had only to discriminate the central lines and respond accordingly; in the remaining 10% of the trials, the sequence was interrupted after the offset of a peripheral stimulus, and participants were asked to indicate, using a digital visual analog scale (VAS; arranged along the vertical axis), the perceived mean position of the peripheral texture just shown on screen. In the inset, the four possible eccentricity levels (5°, 6.5°, 8°, and 9.5° of visual angle) are shown.

Bareket, 2005). The latter component, on the contrary, specifies the distance of the stimulus from fixation, along the angle defined by the azimuth. This information is less precise, and it is more specifically susceptible to changes in attentional control. For this reason, we opted in this study for an experimental design where angular parameters were kept constant, while we systematically varied distance from fixation in the upper visual field. Textures were equiprobably and randomly presented at one of four possible eccentricities along the vertical axis, always in the upper visual field (mean vertical offset for each possible location, calculated from the fixation cross was 5°, 6.5°, 8°, or 9.5° of visual angle, with 1.5° spatial overlap between two contiguous locations; see Figure 1). The use of 1.5° of visual angle as separation between the four peripheral positions was chosen in order to be able to probe both coarse and fine stimulus-localization abilities, as previous research established that the limit between these two “categories” of spatial coding is empirically set around 0.78° or 1° of visual angle (Cohen & Ivry, 1989, 1991).

In order to assess as precisely as possible the ability to localize the spatial position of these textures, a secondary task was introduced, orthogonal to the primary task at fixation: Rarely and unpredictably, the stimulus stream was interrupted after the presentation of a given peripheral stimulus, and participants were required to report, using a continuous visual analog scale (i.e., a digital, vertical VAS was presented on screen), the perceived mean vertical eccentricity of the texture that had just been presented (see Figure 1). Estimations were made using the mouse and a placement of the cursor along the VAS. There was no time pressure for this (secondary) position-estimation task. Once the estimation was validated by the participant, the stimulus presentation resumed. Instructions stressed the importance of being as fast and as accurate as possible for the primary task (i.e., detection of deviant line

orientations at fixation). A total of 200 stimuli per load condition were presented for the central task (for a total of 160 standards, 40 targets). Peripheral stimuli followed central stimulus presentation in 50% of the trials (i.e., 100 per load condition, subdivided into 25 stimuli for each of the four locations, 20 following standard stimuli and five following target stimuli). Each position of the peripheral stimulus was pseudorandomly probed five times per load condition (10% of the total number of trials).

Procedure

Procedure slightly differed between the NA and the neutral groups. All participants were first required to sign an informed consent form, fill out a self-report measure of state anxiety (STAI-S, Spielberger, 1983), and complete a short checklist of personal information (including handedness, possible vision defects and corrections, history of neurological or psychiatric disorders, use of psychoactive medications).

Participants belonging to the NA group also filled in a selection of 10-cm horizontal VASs for mood (energetic, tired, tense, dispirited, happy, satisfied, and angry). Immediately afterward, they were prepared for the electrooculogram recording. Two bipolar leads were positioned above and below the left eyes, and two additional electrodes (Common Mode Sense/Driven Right Leg, working as online reference and ground, Biosemi Active Two System, Amsterdam, the Netherlands, <http://www.biosemi.com>) were applied on the mastoids. Vertical electrooculogram (VEOG) signals were digitized at 512 Hz and stored for further offline analyses. After preparation, participants in this group received task instructions and a short calibration block (20 trials, four targets). During the calibration block, 10 peripheral stimuli were presented during the ISI (eight following nontargets, two per eccentricity

level, plus two following target stimuli). Participants in this group were explicitly told that their performance would be evaluated based on their actual speed and accuracy after the calibration block, and compared with a group of age and education-matched peers. This social comparison took the form of a (bogus) evaluative visual feedback shown on the screen for 20 seconds at the end of the block. We previously showed that this specific manipulation was successful in inducing NA, with corresponding physiological changes compatible with a transient stress response (Rossi & Pourtois, 2012). In addition, this type of affective manipulation was chosen over other types of emotion or mood induction protocols because it has been shown to be ecologically valid, reliable (Nummenmaa & Niemi, 2004), and it provides the added value that it can very easily be integrated with the actual task. Moreover, the targeted change in levels of NA remain fully covert to the participants.

Participants in the neutral condition received task instructions and a short practice block (24 trials) in which they were familiarized with the stimuli, but they did not receive any feedback on their performance, and no mention of an evaluation procedure was made.

After this initial part, all participants received the first test blocks, including 200 trials (160 standards, 40 targets). Then, a new practice block was given to the neutral group (with the central lines oriented in the other direction, as compared with the first half of the experiment, e.g., clockwise). Instead of the practice block, participants in the NA group received a new calibration, and a new bogus negative feedback lasting 20 seconds. Afterward, all participants received new test blocks (200 stimuli). Block order (line orientations and load levels) were fully counterbalanced across participants.

At this point, participants in the neutral group were debriefed.

Participants in the NA group were asked to fill in self-report measures of state anxiety (STAI-S) and mood (VAS), primarily used as manipulation checks for the NA induction procedure. Immediately following these state measures, participants completed an additional block meant to measure volitional saccadic eye movements toward the peripheral textures in the upper visual field. In this block, textures were presented one by one in random order in the upper visual field, and participants had to make a prosaccade each time toward its perceived mean position, and then quickly return with their eyes to fixation (for a similar procedure, see Handy & Khoe, 2005). Stimuli were identical in size and position to the peripheral ones used in the main task, presented 10 times per position (5°, 6.5°, 8°, 9.5° vertical offset), in random order. Every trial started with a brief change in the color of the fixation cross (red, duration 100 ms), signaling the beginning of the preparation period. After one second, a visual texture was presented in one of the four locations for 250 ms, and participants were instructed to move their eyes toward the center of this stimulus and then return their eyes to fixation as fast as possible. To avoid anticipations, some catch trials were used, in which no peripheral stimulus appeared, but a short change in color of the fixation cross itself had to be detected and responded to with a key-press (yellow, 500 ms). Only two catch trials were presented to each participant. After each stimulus (thus, peripheral texture or yellow fixation cross), an interval of between 1500 and 2300 ms elapsed, and then a new trial started (with the fixation cross turning red again).

At the very end of the experimental session, additional trait questionnaires were administered to the participants of the NA group (Ruminative Response Scale, RRS; Behavioral Inhibition System/Behavioral Activation System, BIS/BAS; STAI-T; Emotion Regulation Questionnaire). The RRS data of three participants could not be saved properly, therefore the correlational analyses with RRS scores were based on a sample of 46 participants.

Data Reduction and Analysis

Mean reaction times (RTs) for correct target detections were calculated for the primary task, separately for LL and HL. To test for detection differences across these two load levels, *d prime* scores were also computed, separately for each load. RTs and *d prime* scores were then compared across load and affect conditions using mixed-model repeated-measures ANOVAs with Load (LL, HL, within-subjects) and Affect (neutral, NA, between-subjects) as factors. Performance in the secondary task was calculated as the mean estimation in degrees of visual angle, separately for each of the four eccentricity levels (5°, 6.5°, 8°, 9.5°). These spatial localization estimations were calculated separately for the two Load (LL, HL) and Affect (neutral, NA) conditions, and analyzed with a mixed-model repeated-measures ANOVA with Load (within-subjects), Position (5°, 6.5°, 8°, 9.5°, within-subjects) and Affect (between-subjects) as factors. A closer look at these estimation values, however, suggested that the direction of the estimation error strongly varied depending on the eccentricity level (see Table 1 and Figure 2A). In detail, for textures falling close to fixation, a systematic overestimation of their position in space occurred, whereas for textures in the far periphery, a systematic underestimation was clearly visible, as if participants actually tended to localize positions of the textures toward the center of the display in the upper visual field. To test for the reliability of this observation, we calculated the accuracy of the estimations based on the correct (expected) responses (Prinzmetal et al., 1998; Tsal & Bareket, 1999, 2005). A signed error score (actual response minus correct response) was computed separately for each position, such that negative values corresponded to underestimations of stimulus position, and positive values indicated overestimations. For each position separately, we then tested, using a paired *t* test, whether the error (either over- or underestimation) was significant or not. Next, given that all the error scores were significant (cf. Table 1), but different in direction (sign), suggesting a tendency to misplace the estimations toward the center of the display, we computed a compound accuracy score that could capture this subtle bias (cf. Figure 2A). Inaccuracy and response shift, such as a tendency to perceive stimuli as positioned more closely to the center of the display in conditions of limited attention, have already been reported in the literature (see Chastain, 1986; Prinzmetal et al., 1998), and typically titrated with a compound measure of distance from fixation (which normally overlaps with the center of display). Given the specifics of our design, with fixation not overlapping with the center of the display, we modeled this response shift by fitting a regression line to the four individual mean estimations (one per eccentricity), for each participant and each load level separately (known *x*s: correct responses; known *y*s: actual responses). As a result, a single *b* value and a constant term per load condition were obtained for each participant, allowing a more

Table 1

Mean Estimation Values in Degrees of Visual Angle (SD) for Stimuli Presented at the Four Eccentricity Levels, in Low-Load (LL) and High-Load (HL) Conditions

	LL block	LL error	HL block	HL error
Neutral group ($N = 48$)				
9.5° from fixation	8.8° (0.9) ^a	-0.7° (0.9) ^{***}	8.5° (0.9)	-1.0° (0.9) ^{***}
8° from fixation	7.8° (1.2)	-0.2° (1.2)	7.9° (1.2)	-0.1° (1.2)
6.5° from fixation	7.1° (1.3)	+0.6° (1.3) ^{**}	7.2° (1.0)	+0.7 (1.4) ^{***}
5° from fixation	6.3° (1.2)	+1.3° (1.2) ^{***}	6.5° (1.3)	+1.5° (1.3) ^{***}
NA group ($N = 49$)				
9.5° from fixation	8.3° (1.3)	-1.2° (1.3) ^{***}	8.5° (1.2)	-1.0° (1.2) ^{***}
8° from fixation	7.7° (1.1)	-0.3° (1.1)	7.5° (1.2)	-0.5° (1.2) ^{**}
6.5° from fixation	7.2° (1.0)	+0.7° (1.0) ^{***}	7.0° (1.1)	+0.5 (1.1) ^{**}
5° from fixation	6.3° (1.2)	+1.3° (1.2) ^{***}	6.3° (1.3)	+1.3° (1.3) ^{***}

Note. As can be seen from the mean estimation values, the actual responses were close to the expected responses (cf. Figure 2). However, the error values (actual response minus correct response), expressed in degrees of visual angle (*SD*), were significantly different from zero, indicating lack of precise spatial localization. Negative Error values indicate underestimation of the distance of the stimulus from fixation, and positive values indicate overestimation of this distance.

^a Indicates a significant difference between LL and HL conditions ($p < .05$).

** $p < .01$. *** $p < .001$.

direct estimation of response precision: A slope value of 1 indicated maximal accuracy (minimal shift), and a slope value close to 0 corresponded to higher response shift toward the center of the display. In addition, load and affect-dependent changes in the constant term of the linear regression were analyzed and interpreted as reflecting more consistent response biases: Given equal slopes, a higher constant term would indicate an overall tendency to overestimate the position of the peripheral stimuli across the four positions. Using these derivatives, we compared, using mixed-model repeated-measures ANOVAs with Load (LL, HL) and Affect (neutral, NA) as factors, changes in the fine accuracy of spatial localization of the peripheral textures.

For the Affect group, the vertical electrooculogram recorded from the bipolar electrodes above and below the left eye was segmented in epochs ranging from -100 ms to +800 ms from stimulus onset, separately for the main experimental blocks (dual-task setting) and the additional control block. Trials were baseline-corrected using the entire prestimulus-onset interval (100 ms); epochs contaminated by eyeblinks were semiautomatically detected and rejected based on a criterion of maximum amplitude of $\pm 300 \mu\text{V}$.¹ Average blink-free VEOG traces were calculated separately for stimuli appearing at the four eccentricities, and compared with a 4 (eccentricities) \times 2 (saccade block, task blocks) repeated-measures ANOVA.

The scores obtained from the pre- and postmeasurements of anxiety (STAI-S) were compared with a paired-samples *t* test (two-tailed). The VAS scores were collapsed in a compound VAS for mood (see Rossi & Pourtois, 2011, 2012); the obtained scores (pre- and postmanipulation) were then compared using a two-tailed *t* test.

Results

Manipulation Checks for Negative Affect Induction

Neutral group. The mean STAI-S score at baseline was 35.1 ($SD = 6.3$), which corresponded to a subclinical level of trait anxiety according to published norms (Defares, Van der Ploeg, & Spielberger, 1980).

NA group. STAI-S scores were significantly higher after the experimental session, as compared with the baseline measure ($M_{\text{pre-score}} = 33, SD = 7; M_{\text{postscore}} = 36, SD = 9$), $t(48) = 4.17, p < .001$. In the same direction, the overall negative mood, as captured by the compound VAS, increased significantly from baseline ($M_{\text{pre-score}} = 18.93, SD = 8.6$) to the postsession measurement ($M_{\text{postscore}} = 22.66, SD = 9.42$), $t(48) = 5.16, p < .00001$. Noteworthy was that the postmeasure scores of state anxiety and NA were actually predicted by self-report, trait-like ruminative response style, more specifically by the brooding subscale of the RRS (linear correlation with STAI-S: $r = .35, p = .02$; linear correlation with compound VAS $r = .42, p < .005$, see Table 2). However, no such relationship was found between brooding and the baseline measures of state anxiety or NA, suggesting that a ruminative thinking style could actually worsen the transient experience of negative feelings selectively induced by our bogus feedback manipulation.

Oddball Detection (Primary Task)

As predicted, performance for the task at fixation decreased when perceptual load increased. *D prime* scores were significantly lower in the HL condition ($d' = 1.61, SD = 1.1$) relative to the LL condition ($d' = 2.85, SD = 1.6$), $F(1, 95) = 71.7, p < .0001, \eta_p^2 = .43$), confirming the that the load manipulation was successful. No main effect of affective state, or interactions between affect and load were significant (all *F*s $< .77$, all *p* $> .38$).

¹ Mean rejection rate for the saccade block was 17.0% of the total trials (*S.D.* = 18.0%); mean rejection rates for the LL and HL task blocks were, respectively: 14.3% (17.3%), and 14.3% (15.3%). All comparisons across positions for both saccade block and task blocks were *n.s.* (all $t_{46} < 1.85$, all *p*s $> .07$). The pairwise comparison between saccade block and LL task block was also not significant ($t_{46} = 1.25, p > .21$), nor was the comparison between saccade block and HL task block ($t_{46} = 1.08, p > .28$) or the direct comparison between LL and HL blocks ($t_{46} = 0.04, p > .96$). These results suggest that eye movement behavior (eyeblink rate during trials) was highly comparable between the main experimental blocks (dual task) and the saccade block (and across load levels).

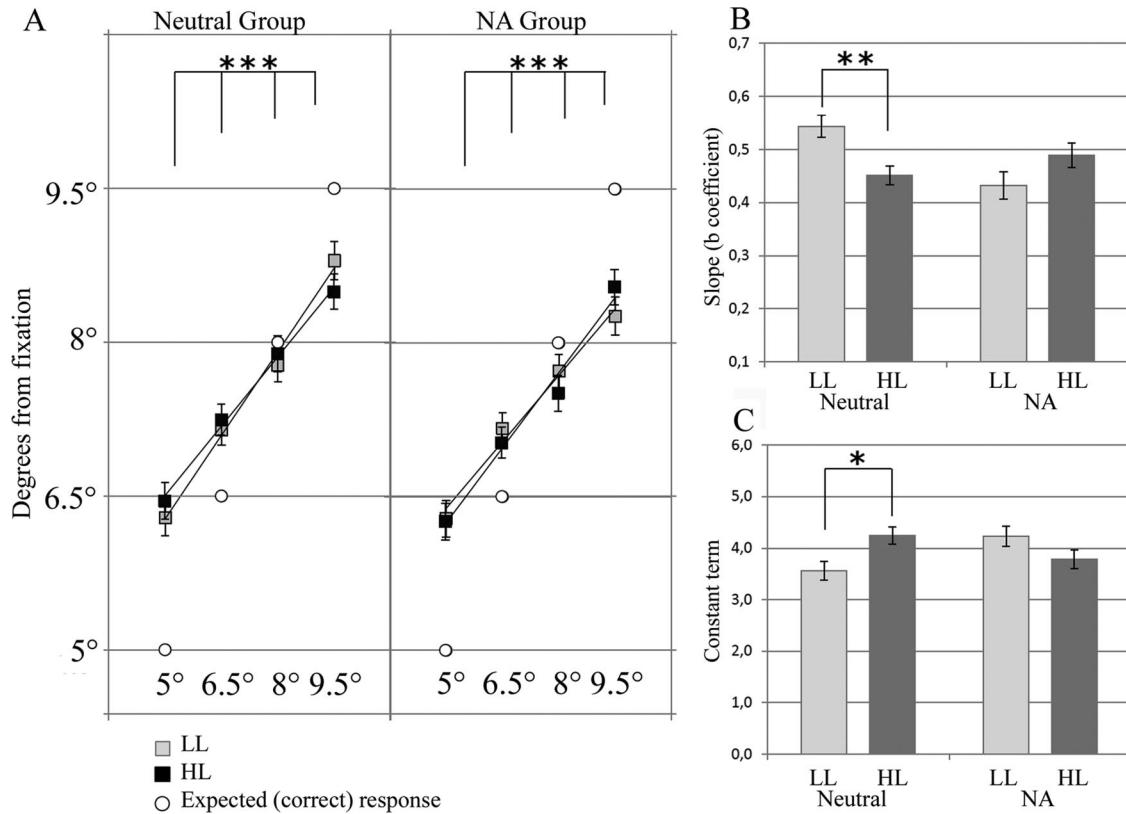


Figure 2. (A) Results for the secondary task. Distribution of mean estimations during the localization task, as a function of eccentricity of the peripheral texture, load level, and affective condition. For textures falling close to fixation, perceived spatial positions were on average overestimated, whereas they were underestimated for textures shown in the far periphery (e.g., 9.5° from fixation). The superimposed trend line corresponds to the fitting of a linear regression line across the four perceived spatial positions, calculated separately for the low-load (LL) and high-load (HL) conditions. The slope was steeper for the LL compared with the HL condition in the neutral group, but this effect was absent in the NA group. (B) A direct comparison of slope values between the two load levels confirmed a significantly lower response shift in the LL compared with the HL condition, only for participants in the neutral group, whereas no significant difference was present in the NA group. (C) Direct comparison between the constant term in LL and HL conditions, separately for participants in the two affective conditions (neutral, NA), illustrating the significant interaction effect Load \times Affect. *** $p < .005$; ** $p < .01$; * $p < .05$; Error bars = 1 SEM.

Likewise, the ANOVA performed on mean RTs for correct target identifications revealed a significant main effect of Load, $F(1, 95) = 61.38$, $p < .0001$, $\eta_p^2 = .39$, indicating slower responses in the HL ($M_{RT} = 639$ ms, $SD = 77$ ms) than in the LL condition ($M_{RT} = 594$ ms, $SD = 63$ ms). A main effect of Affective condition was present on RTs, $F(1, 95) = 7.68$, $p < .01$, $\eta_p^2 = .075$, with overall slower RTs for participants assigned to the NA group ($M_{RTNAGroup} = 634$ ms, $SD = 82$ ms) compared with the neutral group ($M_{RTNeutralGroup} = 599$ ms, $SD = 59$ ms). In addition, the interaction term between Affect and Load was also significant, $F(1, 95) = 6.23$, $p < .05$, $\eta_p^2 = .06$. This interaction was first decomposed by examining if the main effect of load was evidenced in both groups, using two separate one-way ANOVAs. These analyses confirmed that the effect of Load was highly significant in both groups, NA group: $F(1, 48) = 43.27$, $p < .0001$, $\eta_p^2 = .67$; neutral group: $F(1, 47) = 18.83$, $p < .0001$, $\eta_p^2 = .29$. Next, we compared the

effects of the affective state, for each two load levels separately. In the LL condition the two groups did not differ significantly ($M_{RTNAGroup} = 604$ ms, $SD = 70$ ms; $M_{RTNeutralGroup} = 584$ ms, $SD = 53$ ms); $t(95) = 1.63$, $p > .10$, but conversely, in the HL condition, participants in the NA group were significantly slower than participants in the neutral group ($M_{RTNAGroup} = 663$ ms, $SD = 83$ ms; $M_{RTNeutralGroup} = 614$ ms, $SD = 61$ ms); $t(95) = 3.30$, $p < .01$. This effect suggested that participants in the NA group were slightly slower than participants in the neutral group, especially in the HL blocks, but this effect did not account for group differences regarding the processing of the peripheral stimuli (see trade-off analyses here below).

Spatial Localization in the Periphery (Secondary Task)

Figure 2A shows the mean estimations, for each location/eccentricity and load level, separately. These mean estimations confirmed

Table 2
Matrix of Correlation Coefficients Between Trait and State Measures

	STAI-T	RRS-R	RRS-B	RRS-T	ERQ-R	ERQ-S	BIS	BAS-D	BAS-F	BAS-RR
VAS pre	.54**	-.02	.21	.13	-.32*	.10	.09	-.24	.19	-.25
VAS post	.57**	.00	.42**	.19	-.32*	.11	.12	-.15	.19	-.28
STAI-S pre	.62**	-.02	.21	.11	-.21	.15	.23	-.24	.02	-.29*
STAI-S post	.56**	.01	.35*	.23	-.17	.12	.20	-.12	.05	-.24

Note. State measures of anxiety (STAI-S) and NA (VAS) were taken before (pre) and after (post) the affective state manipulation. Trait measures were collected at the end of the experimental session, before final debriefing. Postmanipulation measures of state anxiety and NA were predicted by trait-like ruminative thinking style, in particular the brooding subscale of The RRS (which is specifically related to the negative aspects of self-reflection). As expected, trait anxiety scores (STAI-T) Predicted state anxiety and NA levels. However, this relationship was general, and not specific to the postmanipulation scores. Also reappraisal tendencies (as measured by the reappraisal subscale of the ERQ) showed mild linear relationships with both pre- and post-measures of anxiety, but again this effect was general, and not specific to postscores. VAS = Visual Analogue Scale; STAI-S = State Trait Anxiety Inventory-State part; STAI-T = State Trait Anxiety Inventory-Trait part; RRS-R = Ruminative Response Scale, reflection subscale; RRS-B = Ruminative Response Scale, Brooding subscale; RRS-T = Ruminative Response Scale, Total score; ERQ-R = Emotion Regulation Questionnaire, reappraisal subscale; ERQ-S = Emotion Regulation Questionnaire, suppression subscale; BIS = Behavioral Inhibition System; BAS-D = Behavioral Activation System, drive subscale; BAS-F = Behavioral Activation System, fun-seeking subscale; BAS-RR = Behavioral Activation System, reward responsiveness subscale.

* $p < .05$. ** $p < .01$.

that for each load level, participants did not make random estimations, but their decisions were strongly influenced by the actual position of the texture shown in the upper visual field (see Table 1). When calculating the average estimations for each participant at each location, results confirmed that the mean response differed significantly across positions, main effect of Position: $F(3, 285) = 174.22, p < .0001, \eta_p^2 = .65$. All pairwise comparisons were significant (all $t(96) > 6.82$, all $p < .00001$). These results confirmed that, regardless of load level or affective state, spatial localization for the four positions was fairly accurate, as demonstrated by a clear four-modal distribution of the responses along the vertical meridian/axis. In addition, the analysis showed a significant three-way interaction for Load \times Position \times Affect, $F(3, 285) = 4.97, p < .005, \eta_p^2 = .05$. This interaction was explained by a higher accuracy in the LL compared with the HL condition ($M_{LL} = 8.8^\circ, SD = 0.9^\circ; M_{HL} = 8.5^\circ, SD = 0.9^\circ$); $t(47) = 2.64, p < .05$ only in the neutral group for the most eccentric position (9.5°), whereas at all other positions, no difference in accuracy was evidenced between the two load levels: all $t(47) < 1.36$, all $ps > .17$ or between the two groups (all $ts < 1.51$, all $ps > .13$).

Statistical analyses carried out on the raw error values (see Table 1) showed that error estimations were significantly different from zero in all four positions, all $t(96) > |2.44|$, all $ps < .05$, changing sign (direction) depending on the actual eccentricity. This effect reflects a tendency to compress (shift) the estimations toward the center of the display. Crucially, this effect is influenced by load and emotion concurrently. The statistical analysis performed on the response shift measure (i.e., slope values) revealed a significant interaction effect between Load and Affect, $F(1, 95) = 8.89, p < .004, \eta_p^2 = .098$. This interaction was then decomposed by means of one-way ANOVAs (with Load as main factor), carried out separately for the two groups (neutral and NA, see Figure 2B). In the neutral group, a significantly steeper slope was observed in the LL condition ($M_b = 0.54, SD = 0.29$) compared with the HL condition ($M_b = 0.45, SD = 0.25$); $F(1, 47) = 7.99, p < .01, \eta_p^2 = .15$. This effect translated a significantly stronger response shift toward the center of the display (central bias) for peripheral textures in the HL, compared with the LL condition. Additional bivariate correlational analyses were performed to assess whether levels of state anxiety at baseline

(neutral group) could potentially account for some of the interindividual variability observed on these slope scores, and whether this effect (central bias) could be explained by a systematic change of performance during the primary task (i.e., tradeoff effects between the two tasks). Consistent with the prediction that levels of anxiety would influence localization abilities, we found across participants significant negative correlations between slope values and STAI-S scores, both for LL ($r = .30, p < .05$) and HL ($r = .31, p < .05$). These linear correlations (see Figure 3) indicated that, regardless of load level, higher levels of state anxiety (measured at baseline, thus completely unrelated to the task at hand) were associated with shallower slopes (i.e., closer to 0), hence with increased response shift. Moreover, all correlations carried out between slope values and performance indices for the primary task were nonsignificant (all $rs < |.26|$, $ps > .07$), suggesting that load-dependent changes observed for the secondary task were not merely explained by tradeoff effects with the primary task.

Importantly and by contrast, in the NA group, no significant difference was evidenced between the two load levels, $F(1, 47) =$

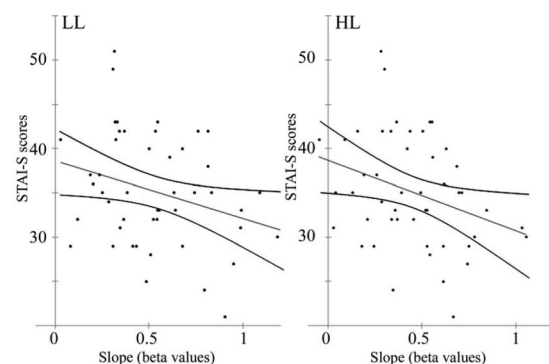


Figure 3. Scatterplots for the significant correlations (neutral group) performed across participants between baseline levels of state-anxiety and beta values (i.e., slope coefficients) obtained after the fitting of a regression line across the four position estimations (confidence interval for the mean 95%). The Pearson coefficient was significant both for the LL (left panel) and the HL condition (right panel).

2.26, $p > .14$, $\eta_p^2 < .05$; HL condition: $\beta = 0.49$, $SD = 0.32$; LL condition: $\beta = 0.43$, $SD = 0.36$. Hence, during the experience of NA, spatial localization abilities for the peripheral textures were as imprecise in the LL as in the HL condition. Similar to the neutral group, no tradeoff effect between the two tasks was observed (all $r_s < 1.161$, $p_s > .27$).

These findings, suggesting an interaction effect between perceptual load and NA during the fine spatial localization of peripheral textures, were further substantiated by statistical analyses carried out on the constant term of the linear equation (cf. Figure 2C). The ANOVA confirmed a significant Load \times Affect interaction effect, $F(1, 95) = 8.27$, $p = .005$, $\eta_p^2 = .08$. This interaction was then further decomposed by means of one-way ANOVAs (Load as factor), carried out separately for the two groups (neutral and NA). In the neutral group, a significantly lower constant term was observed in the LL condition ($M_{\text{constant}} = 3.56$, $SD = 2.56$) compared with the HL condition ($M_{\text{constant}} = 4.25$, $SD = 2.33$); $F(1, 47) = 6.78$, $p < .05$, $\eta_p^2 = .13$. Crucially however, this difference was not observed in the NA group, $F(1, 48) = 2.31$, $p > .13$, $\eta_p^2 < .05$; $M_{\text{constantLL}} = 4.23$, $SD = 2.77$; $M_{\text{constantHL}} = 3.79$, $SD = 2.57$, showing an NA-dependent lowering of fine spatial localization abilities, even though load (at fixation) was low.

Eye-Movement Behavior: Saccade Block Versus Test Blocks

As can be seen in Figure 4, the size of the saccadic movement was accurately traced by the oculogram during the voluntary saccade task: The larger the distance between initial fixation and position of the texture in the upper visual field, the larger the amplitude of the VEOG signal. A statistical analysis carried out on these amplitude values showed a significant main effect of Position, $F(3, 138) = 35.58$, $p < .0001$, $\eta_p^2 = .44$, which was explained by significant amplitude differences across all positions (see Table 3; all $t_{s_{46}} > 2.6$, all $p_s < .05$). When the same analysis was performed on the VEOG amplitude data recorded during the main task (in which fixation was required), no significant effect of Position, $F(3, 138) = 0.52$, $p > .66$, $\eta_p^2 = .01$, or Load, $F(1, 46) = 0.51$, $p > .48$, $\eta_p^2 = .01$ was evidenced. These results confirmed that participants did not make obvious saccadic movements toward the peripheral textures during the main experiment, but their eyes were carefully monitoring the RSVP taking place at fixation; hence, the spatial position of the textures was processed using peripheral vision.

Discussion

Our results show that enhancing perceptual load in a task at fixation reliably impaired performance in a secondary task performed with peripheral stimuli, as previously reported in the literature for visual awareness (Macdonald & Lavie, 2008). In the absence of tradeoff effects between the two tasks, we found that participants in the neutral emotional group were worse in the HL condition in precisely estimating the actual position of peripheral textures shown in the upper visual field, compared with the LL condition. This new result replicates and extends earlier work showing similar effects for localization tasks (Tsal & Bareket, 2005). However, it is crucial to note, we found that this effect was state-dependent. More specifically, we found that in the NA group, the gain disappeared in the fine spatial localization of the periph-

eral stimuli when load (at fixation) was low, compared with a high-load condition, as if NA imposed an extra attentional bottleneck on perceptual abilities.

Coarse Versus Fine Spatial Encoding Under Load and NA

Previous research already showed that (covert) attention allocation is needed for precise object localization (Newby & Rock, 2001; Prinzmetal et al., 1998; Tsal & Bareket, 1999). Stimuli losing the competition for attention, for whatever reason, are usually localized less accurately than stimuli that benefit from a prioritized attention selection. However, it has previously been shown that spatial localization is still fairly accurate in minimally attended conditions (Tsal & Bareket, 2005), but a finer discrimination of spatial positions may be lost due to the properties of (adaptive) attentional receptive fields (ARF, Shalev & Tsal, 2002), because access to their output functions depends on the amount of attention resources available at a given time.

Here, we provide evidence confirming that coarse coding of the position of peripheral stimuli was still preserved despite conditions taxing processing resources (HL and/or NA). In other words, even though attention resources were primarily allocated to a demanding task at fixation (HL level) or NA was reliably induced, participants' responses in the peripheral task were not scattered randomly in the upper visual field, but, instead, they clustered according to the actual positions of the textures, as computational models of perception postulate (Yuille & Grzywacz, 1989). It is important to note, by monitoring saccadic eye movements along the vertical axis, we could ascertain that the maintained coarse coding of stimulus position could not be explained by differential eye movements or obvious visuomotor ocular strategies.

Also of note, we were able to collect evidence supporting the idea that attention is needed for accessing the most precise ARF output: Perceptual load, as well as NA, worsened the fine spatial localization of the peripheral textures, as suggested by higher estimation errors in the far position, lower beta scores, and higher constant terms in the linear equation modeling of the estimations. The similarity of these two effects (load and affect) suggests that in both situations, important attentional resources are presumably consumed by other processes (e.g., emotion regulation), and in turn made unavailable for localizing with precision the actual position of the texture in the upper visual field.

At the neurophysiological level, these results are compatible with a classical attentional-gating phenomenon, operating in early visual cortices (Hillyard & Anllo-Vento, 1998; Kastner & Ungerleider, 2000; Luck, Hillyard, Mouloua, Woldorff, Clark, & Hawkins, 1994). In this framework, under LL (hence when some attentional capacity is left over), the peripheral stimuli might elicit stronger activations in early visual cortices, including in V1 (Rauss et al., 2009; Rees et al., 1997; Rossi & Pourtois, 2012; Schwartz et al., 2005). In this area, attention had been previously shown to boost signal strength and sharpen position tuning (Fischer & Whitney, 2009), eventually enhancing spatial resolution (Carrasco & Yeshurun, 2009; Yeshurun & Carrasco, 1998). By comparison, under HL, given that the residual attentional capacity is reliably reduced (Lavie, 2005), early visual responses are also significantly decreased (see Rauss et al., 2009; Schwartz et al., 2005 for converging evidence of an early modulation of V1 using a similar

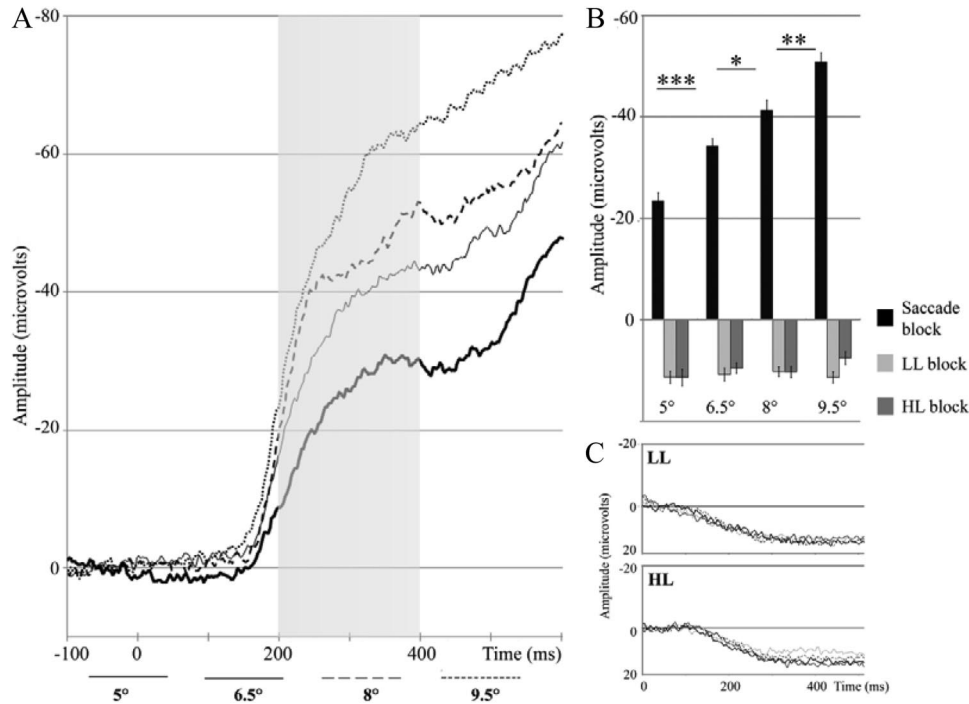


Figure 4. (A) Average VEOG amplitudes as a function of eccentricity of the peripheral texture during the control block that required volitional vertical saccades. The amplitude of the VEOG increased linearly with increasing distance from fixation (and accordingly, the amplitude of the corresponding saccadic movement). (B) Pairwise comparisons performed on the mean amplitude values of the VEOG (calculated between 200 and 400 ms poststimulus onset; see shaded area in Figure 4 A) during the control block confirmed a monotonic increase in amplitude as a function of increasing eccentricity. By comparison, during the main experimental session, regardless of the load level, no similar change in the mean amplitude of the VEOG could be evidenced (all comparisons = *ns*). Error bars indicate 1 *SD*. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. (C) This latter conclusion was further corroborated by the analysis of the VEOG time-course during the main experimental session, separately for load level (2) and eccentricity (4).

task), and spatial resolution eventually decreased. Based on our new results, we can also conclude that task-related factors (e.g., load) are not the only ones at play in defining the amount of free-floating attentional resources that can still be deployed to peripheral stimuli: NA seems as effective as load in consuming attentional capacity, therefore causing changes in spatial attention, as reported previously in works showing a reduction of the attentional breadth following the induction of (or confrontation with) NA (Easterbrook, 1959; Fenske & Eastwood, 2003; Finucane &

Powers, 2010; Gable & Harmon-Jones, 2010). More generally, our novel behavioral results enable us to bridge the gap between computational models of location perception, changes in early primary visual cortex excitability as a function of attention and negative affect (C1 component, see Rossi & Pourtois, 2012), and corresponding alterations in fine-grained spatial localization abilities that can be measured at the behavioral level.

Structural Versus State-Dependent Effects on Early Spatial Perception

Even though effects of NA on spatial localization abilities mimic effects of perceptual load at first sight, the brain networks underlying these modulatory effects on early spatial vision may be different. Load effects are classically ascribed to dorsal brain pathways, involving primarily fronto-parietal, top-down attention-control networks (Bishop, 2009; Culham, Cavanagh, & Kanwisher, 2001; Schwartz et al., 2005; Tomasi et al., 2011), which in turn gate information processing in distant sensory areas (including V1), possibly by biasing neuronal excitability (Muggleton, Lamb, Walsh, & Lavie, 2008). By comparison, negative affective state could bias early sensory perception (here, spatial localization) via neural changes in a different route, including ventral brain

Table 3

VEOG Mean Amplitudes Recorded During the Saccade (Control) Block and During the Main Task Blocks (With a Distinction Between the LL and HL Condition)

	Saccade block	LL block	HL block
9.5° from fixation	-50.9 (24.5)	10.3 (15.4)	7.5 (17.2)
8° from fixation	-41.4 (25.6)	11.4 (22.0)	9.6 (14.1)
6.5° from fixation	-34.3 (18.3)	10.2 (13.0)	11.4 (15.2)
5° from fixation	-23.5 (20.7)	11.3 (20.7)	10.8 (20.7)

Note. In both cases, the exact same peripheral stimuli were used. Shown at four different eccentricities along the vertical meridian. Values are provided in μV (*SD*).

structures, the amygdala and medial prefrontal cortex (Pourtois et al., 2012). Two findings reported in our study indirectly support this dissociation. First, we found a positive correlation between increases in levels of state anxiety after the encounter of the negative feedback challenging self-efficacy and brooding as a trait-like predisposition. This observation suggests that our induction of NA likely tapped into specific affective processes, implicated in emotion (dis)regulation and self-focused attention. The proneness to ruminative responses has been linked to increased activations in prefrontal regions related to self-focused attention as well as in the amygdala during the experience of increased NA (Ray, Ochsner, Cooper, Robertson, Gabrieli, & Gross, 2005). Accordingly, NA effects in our study are very likely related to changes in this affective circuit, as opposed to a more dorsal fronto-parietal network in the case of perceptual load and endogenous attention control. This conjecture is also in line with recent neuroimaging results showing enhanced long-lasting connectivity between amygdala and fronto-parietal self-related areas after social stress (Veer, Oei, Spinhoven, van Buchem, Elzinga, & Rombouts, 2011). Second, shifts toward activations in ventral (limbic) “affective” structures, as compared with more dorsal/cognitive areas, have repeatedly been observed during tasks performed under social stress or threat encounter (Drevets & Raichle, 1998; Oei, Veer, Wolf, Spinhoven, Rombouts, & Elzinga, 2011). Therefore, it is plausible to assume that such a ventral emotional network (with a tonic activation throughout our task) might account for the emotion-dependent drop in spatial localization abilities. In this framework, a load-like effect on early spatial localization produced by the transient experience of NA would essentially be explained by the concurrent activation of ventral brain structures involved in emotional regulation processes, rather than by changes in the fronto-parietal network involved in the endogenous control of attention. These ventral “affective” structures comprise the amygdala, which might directly bias activations in V1, given its strong reciprocal anatomical connections with early visual areas (Amaral, Behnia, & Kelly, 2003; Gschwind, Pourtois, Schwartz, De Ville, & Vuilleumier, 2012; Pourtois et al., 2012; Vuilleumier, 2005). Alternatively, early modulation of spatial perception by NA could also be explained by the activation of more posterior brain areas, which are involved in self-referential thinking, such as the precuneus (Cavanna & Trimble, 2006 for a review), or the posterior cingulate cortex (Vogt, Vogt, & Laureys, 2006), heavily connected to the occipital lobe and early visual areas.

Although the results of this study are broadly consistent with dominant cognitive models (Lavie, 2005) and neuroimaging data (Schwartz et al., 2005; Schmitz et al., 2009), a few limitations have to be pointed out. First, based on the present findings and experimental design, we cannot conclude that the (preserved) coarse spatial coding (under HL or NA) of the peripheral textures was actually performed without (selective) attention, mainly because we probed, albeit rarely, their conscious perception, making them somewhat task relevant. However, due to the similarities between the present experiment paradigm and earlier studies in which the processing of the peripheral stimuli remained covert, we feel rather confident that our results for perceptual load and NA can be ascribed to the allocation of *limited* residual attentional capacity, in line with push-pull models of attentional deployment (Pinsk, Doninger & Kastner, 2004).

Second, in our study, spatial localization abilities were investigated for the upper visual field, exclusively. This choice was primarily motivated by practical considerations (e.g., time constraints, related to the necessity to probe various stimulus locations only rarely), as well as theoretical reasons. Previous ERP studies (Pourtois, Rauss, Vuilleumier, & Schwartz, 2008; Rauss et al., 2009) showed that the attentional modulation of early sensory processing for large peripheral stimuli (textures) was larger in the upper compared with the lower visual field. This asymmetry may stem from differences in spatial resolution and contrast sensitivity across these two different parts of the visual field (Abrams, Nizam, & Carrasco, 2012; Skrandies, 1985). Future studies are needed to assess whether the early attention-gating effect observed in this study during spatial vision (and caused either by HL or NA state) might be obtained equally for textures shown in the lower (as opposed to upper) visual field. Last, our results are based on a very specific NA induction procedure, and our interpretations concerning the effects of emotional state on visual perception are primarily based on the assumption of NA exerting an early attention bottleneck, causing competition for attention allocation. In this context, it appears valuable to compare effects of this specific NA manipulation on early spatial perception to other types of NA induction classically used in the literature (e.g., film clips, picture exposure, or threat of shock). Moreover, future studies are needed to explore whether or not, by contrast, positive affective states could actually soften this competition, given the putative boost in attentional capacity and more specifically the broadening of the attentional focus usually associated with positive emotion (see Fredrickson, 2004; Vanlessen et al., *in press*).

Conclusion

In sum, results of this study show that spatial perception depends not only upon structural attentional factors, but also state-dependent affective variables. Under LL, presumably when residual attention capacity was still available, participants were better at localizing the precise position of peripheral textures shown in the upper visual field, compared with a condition where these residual attention capacity was consumed by a demanding task at fixation (HL). This load-dependent effect was not related to a change in the coarse spatial coding of these textures, but rather to a drop in their fine localization, and hence presumably the spatial resolution in the upper visual field. Remarkably, a very similar effect was evidenced when participants experienced enhanced levels of NA, even when attention capacity was not exhausted. Altogether, these new results suggest that spatial perception is shaped by multiple attention-control mechanisms. A decreased spatial localization ability for stimuli shown in the periphery can result equally from the engagement in an orthogonal demanding task or from (intrusive) negative thoughts. Both phenomena presumably deplete central attentional capacity, even though the underlying brain networks responsible for these two effects might be nonoverlapping.

References

- Abrams, J., Nizam, A., & Carrasco, M. (2012). Isoeccentric locations are not equivalent: The extent of the vertical meridian asymmetry. *Vision Research*, 52, 70–78. doi:10.1016/j.visres.2011.10.016
- 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, 1099–1120. doi:10.1016/S0306-4522(02)01001-1
- Bishop, S. J. (2009). Trait anxiety and impoverished prefrontal control of attention. *Nature Neuroscience*, 12, 92–98. doi:10.1038/nn.2242
- Carrasco, M., & Yeshurun, Y. (2009). Covert attention effects on spatial resolution. *Progress in Brain Research*, 176, 65–86. doi:10.1016/S0079-6123(09)17605-7
- Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain: A Journal of Neurology*, 129, 564–583. doi:10.1093/brain/awl004
- Chajut, E., & Algom, D. (2003). Selective attention improves under stress: implications for theories of social cognition. *Journal of Personality and Social Psychology*, 85, 231–248. doi:10.1037/0022-3514.85.2.231
- Chastain, G. (1986). Evidence for feature perturbations from character misidentifications. *Perception & Psychophysics*, 39, 301–306. doi:10.3758/BF03204940
- Clark, V. P., Fan, S., & Hillyard, S. A. (1994). Identification of early visual evoked potential generators by retinotopic and topographic analyses. *Human Brain Mapping*, 2, 170–187. doi:10.1002/hbm.460020306
- Cohen, A., & Ivry, R. (1989). Illusory conjunctions inside and outside the focus of attention. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 650–663. doi:10.1037/0096-1523.15.4.650
- Cohen, A., & Ivry, R. B. (1991). Density effects in conjunction search: Evidence for a coarse location mechanism of feature integration. *Journal of Experimental Psychology: Human Perception and Performance*, 17, 891–901. doi:10.1037/0096-1523.17.4.891
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3, 201–215. doi:10.1038/nrn755
- Culham, J. C., Cavanagh, P., & Kanwisher, N. G. (2001). Attention response functions: Characterizing brain areas using fmri activation during parametric variations of attentional load. *Neuron*, 32, 737–745. doi:10.1016/S0896-6273(01)00499-8
- Defares, P. B., Van der Ploeg, H. M., & Spielberger, C. D. (1980). *Handleiding bij de Zelf-Beoordelingsvragenlijst (ZBV): Een nederlandse bewerking van de Spielberger State-Trait Anxiety Inventory*. Lisse, the Netherlands: Swets & Zeitlinger.
- Drevets, W. C., & Raichle, M. E. (1998). Reciprocal suppression of regional cerebral blood flow during emotional versus higher cognitive processes: Implications for interactions between emotion and cognition. *Cognition & Emotion*, 12, 353–385. doi:10.1080/026999398379646
- Easterbrook, J. A. (1959). The effect of emotion on cue utilization and the organization of behavior. *Psychological Review*, 66, 183–201. doi:10.1037/h0047707
- Fenske, M. J., & Eastwood, J. D. (2003). Modulation of focused attention by faces expressing emotion: evidence from flanker tasks. *Emotion*, 3, 327–343. doi:10.1037/1528-3542.3.4.327
- Finucane, A. M., & Power, M. J. (2010). The effect of fear on attentional processing in a sample of healthy females. *Journal of Anxiety Disorders*, 24, 42–48. doi:10.1016/j.janxdis.2009.08.005
- Fischer, J., & Whitney, D. (2009). Attention narrows position tuning of population responses in V1. *Current Biology*, 19, 1356–1361. doi:10.1016/j.cub.2009.06.059
- 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, 139–150. doi:10.1007/s00221-001-0906-7
- Fredrickson, B. L. (2004). The broaden-and-build theory of positive emotions. *Philosophical Transactions of the Royal Society of London: Series B. Biological Sciences*, 359, 1367–1378. doi:10.1098/rstb.2004.1512
- Gable, P., & Harmon-Jones, E. (2010). The blues broaden, but the nasty narrows. *Psychological Science*, 21, 211–215. doi:10.1177/0956797609359622
- Gschwind, M., Pourtois, G., Schwartz, S., Van De Ville, D., & Vuilleumier, P. (2012). White-matter connectivity between face-responsive regions in the human brain. *Cerebral Cortex*, 22, 1564–1576. doi:10.1093/cercor/bhr226
- Handy, T. C., & Khoe, W. (2005). Attention and sensory gain control: A peripheral visual process? *Journal of Cognitive Neuroscience*, 17, 1936–1949. doi:10.1162/089892905775008715
- Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences*, 95, 781–787. doi:10.1073/pnas.95.3.781
- 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, 1–21. doi:10.1007/BF00233372
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, 23, 315–341. doi:10.1146/annurev.neuro.23.1.315
- Lavie, N. (1995). Perceptual load as a necessary condition for selective attention. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 451–468. doi:10.1037/0096-1523.21.3.451
- Lavie, N. (2005). Distracted and confused?: Selective attention under load. *Trends in Cognitive Sciences*, 9, 75–82. doi:10.1016/j.tics.2004.12.004
- Lavie, N., & Tsal, Y. (1994). Perceptual load as a major determinant of the locus of selection in visual attention. *Perception, & Psychophysics*, 56, 183–197. doi:10.3758/BF03213897
- Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: Psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 887–904. doi:10.1037/0096-1523.20.4.887
- Macdonald, J. S. P., & Lavie, N. (2008). Load induced blindness. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 1078–1091. doi:10.1037/0096-1523.34.5.1078
- Muggleton, N., Lamb, R., Walsh, V., & Lavie, N. (2008). Perceptual load modulates visual cortex excitability to magnetic stimulation. *Journal of Neurophysiology*, 100, 516–519. doi:10.1152/jn.01287.2007
- Newby, E. A., & Rock, I. (2001). Location and attention. *The Quarterly Journal of Experimental Psychology: A. Human Experimental Psychology*, 54, 155–168. doi:10.1080/02724980042000066
- Nummenmaa, L., & Niemi, P. (2004). Inducing affective states with success–failure manipulations: A meta-analysis. *Emotion*, 4, 207–214. doi:10.1037/1528-3542.4.2.207
- Oei, N. Y. L., Veer, I. M., Wolf, O. T., Spinhoven, P., Rombouts, S. A. R. B., & Elzinga, B. M. (2011). Stress shifts brain activation towards ventral ‘affective’ areas during emotional distraction. *Social Cognitive and Affective Neuroscience*. Advance online publication. doi:10.1093/scan/nsr024
- Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a ‘low road’ to ‘many roads’ of evaluating biological significance. *Nature Reviews Neuroscience*, 11, 773–783. doi:10.1038/nrn2920
- Pinsk, M. A., Doniger, G. M., & Kastner, S. (2004). Push-pull mechanism of selective attention in human extrastriate cortex. *Journal of Neurophysiology*, 92, 622–629. doi:10.1152/jn.00974.2003
- Pourtois, G., Rauss, K. S., Vuilleumier, P., & Schwartz, S. (2008). Effects of perceptual learning on primary visual cortex activity in humans. *Vision Research*, 48, 55–62. doi:10.1016/j.visres.2007.10.027
- Pourtois, G., Schettino, A., & Vuilleumier, P. (2012). Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. *Biological Psychology*. Advance online publication. doi:10.1016/j.biopsycho.2012.02.007
- Prinzmetal, W., Amiri, H., Allen, K., & Edwards, T. (1998). The phenomenology of attention: Part I. Color, location, orientation, and spatial frequency. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 261–282. doi:10.1037/0096-1523.24.1.261

- Rauss, K. S., Pourtois, G., Vuilleumier, P., & Schwartz, S. (2009). Attentional load modifies early activity in human primary visual cortex. *Human Brain Mapping, 30*, 1723–1733. doi:10.1002/hbm.20636
- Rauss, K. S., Schwartz, S., & Pourtois, G. (2011). Top-down effects on early visual processing in humans: A predictive coding framework. *Neuroscience & Biobehavioral Reviews, 35*, 1237–53. doi:10.1016/j.neubiorev.2010.12.011
- Ray, R. D., Ochsner, K. N., Cooper, J. C., Robertson, E. R., Gabrieli, J. D. E., & Gross, J. J. (2005). Individual differences in trait rumination and the neural systems supporting cognitive reappraisal. *Cognitive, Affective & Behavioral Neuroscience, 5*, 156–168. doi:10.3758/CABN.5.2.156
- Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science, 278*, 1616–1619. doi:10.1126/science.278.5343.1616
- Rossi, V., & Pourtois, G. (2011). Transient state-dependent fluctuations in anxiety measured using STAI, POMS, PANAS or VAS: A comparative review. *Anxiety, Stress & Coping, 25*, 603–645. doi:10.1080/10615806.2011.582948
- Rossi, V., & Pourtois, G. (2012). State-dependent attention modulation of human primary visual cortex: A high density ERP study. *NeuroImage, 60*, 2365–2378. doi:10.1016/j.neuroimage.2012.02.007
- Schmitz, T. W., De Rosa, E., & Anderson, A. K. (2009). Opposing influences of affective state valence on visual cortical encoding. *The Journal of Neuroscience, 29*, 7199–7207. doi:10.1523/JNEUROSCI.5387-08.2009
- 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*, 770–786. doi:10.1093/cercor/bhh178
- Shalev, L., & Tsai, Y. (2002). Detecting gaps with and without attention: Further evidence for attentional receptive fields. *European Journal of Cognitive Psychology, 14*, 3–26. doi:10.1080/09541440143000005
- Skrandies, W. (1985). Human contrast sensitivity: Regional retinal differences. *Human Neurobiology, 4*, 95–97.
- Spielberger, C. D. (1983). *Manual for the State-Trait Anxiety Inventory (Form Y) Self-Evaluation Questionnaire*. Palo Alto, CA: Consulting Psychologists Press.
- Tomasi, D., Volkow, N. D., Wang, G. J., Wang, R., Telang, F., Caparelli, E. C., . . . Fowler, J. S. (2011). Methylphenidate enhances brain activation and deactivation responses to visual attention and working memory tasks in healthy controls. *NeuroImage, 54*, 3101–3110. doi:10.1016/j.neuroimage.2010.10.060
- Tsal, Y., & Bareket, T. (1999). Effects of attention on localization of stimuli in the visual field. *Psychonomic Bulletin & Review, 6*, 292–296. doi:10.3758/BF03212332
- Tsal, Y., & Bareket, T. (2005). Localization judgments under various levels of attention. *Psychonomic Bulletin & Review, 12*, 559–566. doi:10.3758/BF03193805
- Vanlessen, N., Rossi, V., De Raedt, R., & Pourtois, G. (in press). Positive emotion broadens attention focus through decreased position-specific spatial encoding in early visual cortex: Evidence from ERPs. *Cognitive, Affective and Behavioral Neuroscience*.
- Veer, I. M., Oei, N. Y. L., Spinhoven, P., van Buchem, M. A., Elzinga, B. M., & Rombouts, S. A. R. B. (2012). Endogenous cortisol is associated with functional connectivity between the amygdala and medial prefrontal cortex. *Psychoneuroendocrinology*. Online publication. doi:10.1016/j.psyneuen.2011.12.001
- Vogt, B. A., Vogt, L., & Laureys, S. (2006). Cytology and functionally correlated circuits of human posterior cingulate areas. *NeuroImage, 29*, 452–466. doi:10.1016/j.neuroimage.2005.07.048
- Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences, 9*, 585–594. doi:10.1016/j.tics.2005.10.011
- Wessel, I., & Merckelbach, H. (1997). The impact of anxiety on memory for details in spider phobics. *Applied Cognitive Psychology, 11*, 223–231. doi:10.1002/(SICI)1099-0720(199706)11:3<223::AID-ACP444>3.0.CO;2-4
- World Medical Association. (2008). *Ethics of human experimentation*. Retrieved from <http://www.wma.net/en/30publications/10policies/b3/17c.pdf>
- Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature, 396*, 72–75. doi:10.1038/23936
- Yuille, A. L., & Grzywacz, N. M. (1989). A winner-take-all mechanism based on presynaptic inhibition. *Neural Computation, 1*, 334–347. doi:10.1162/neco.1989.1.3.334

Received June 1, 2012

Revision received August 13, 2012

Accepted October 1, 2012 ■