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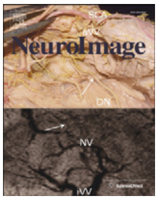

State-dependent attention modulation of human primary visual cortex: A high density ERP study

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Converging electrophysiological and brain-imaging results show that sensory processing in V1 can be modulated by attention. In this study, we tested the prediction that this early filtering effect depends on the current affective state of the participant. We recorded visual evoked potentials (VEPs) to visual peripheral distractors while participants performed a demanding task at fixation, whose perceptual load was manipulated in a parametric fashion. Crucially, levels of negative affect were either increased or decreased independently of changes in perceptual load. Concurrent psychophysiological measurements and self-report scales confirmed that changes in emotional state were effective. In the control condition, ERP results showed that the C1 component generated in response to the exact same peripheral distractors systematically varied in amplitude with the amount of perceptual load imposed at fixation, being larger when perceptual load decreased. However, this early modulatory effect in V1 was disrupted when participants transiently experienced increased state anxiety, resulting in a decreased C1 amplitude even though task load at fixation remained low. These results suggest that early bottom-up processing in V1 is not only influenced by the amount of attention resources available, but also by the current internal state of the participant.

Introduction

Permeability of human V1 to cognitive factors

A growing number of studies provides evidence for the permeability of sensory processing within the human primary visual cortex (V1) to higher-order top-down cognitive effects, including learning, attention or stimulus predictability (Alink et al., 2010; Hopf et al., 2004; O'Connor et al., 2002; Poghosyan and Ioannides, 2008; Poghosyan et al., 2005). At the electrophysiological level, reliable stimulus-related activation of V1 is classically assessed in humans by recording the first cortical component of the Visual Evoked Potentials (VEPs), the retinotopic C1. This component usually peaks ~50–100 ms post-stimulus onset over occipito-parietal leads, and its main generators are classically ascribed to pyramidal neurons of layers III and V covering the fundus of the calcarine fissure (Clark et al., 1995; Di Russo et al., 2002; Foxe and Simpson, 2002; Jeffreys and Axford, 1972). The C1 has for a long time been described as being resistant to modulatory effects exerted by distant fronto-parietal attention control regions onto lower tier visual cortex (Clark and Hillyard, 1996; Handy et al., 2001; Martinez et al., 1999). More recently, systematic C1 amplitude changes have been reported with top-down cognitive manipulations (see Rauss et al., 2011 for a recent review), including perceptual learning and expertise (Bao et al., 2010; Jin et al., 2010; Pourtois et al., 2008), emotional valence (Eldar et al., 2010; Halgren et al., 2000; Pourtois et al., 2004; West et al., 2011), and feature-based or spatial attention (Karns and Knight, 2009; Kelly et al., 2008; Proverbio et al., 2010; Zani and Proverbio, 2009). With regards to attention, not only increases of the C1 to attended visual stimuli were shown, but also substantial reductions of this same early visual component to unattended or task-irrelevant stimuli were evidenced, suggesting flexible and adaptive gain control mechanisms exerted by putative fronto-parietal networks onto lower tier visual cortex, including V1 (Slotnick et al., 2003). Moreover, in line with theories and results suggesting that the first sweep of bottom-up cortical processing in V1 may be gated as a function of attentional capacity (see Desseilles et al., 2009; Lavie, 2005; Rees et al., 1997; Schwartz et al., 2005), recent ERP findings confirmed that increases in perceptual load reliably reduced the amplitude of the C1 recorded in response to (unattended) peripheral visual distractors (Rauss et al., 2009). Hence, attentional control mechanisms can exert top-down modulatory effects in early sensory cortex, including in V1.

Permeability of V1 to affective factors

However, not only attention selection, but also the internal state of the participant at a given time can influence low-level encoding of the incoming visual stimulus, as early as in V1 (Supèr et al., 2003), and hence presumably the C1 component. Consistent with this view, in a previous ERP study, Stolarova et al. (2006) reported amplitude changes of the C1 to gratings as a function of aversive

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conditioning. These early modulatory effects taking place in V1 rapidly following stimulus onset may be caused by direct feedback effects exerted from distant deep limbic structures, like the amygdala, onto the occipital cortex, including V1 (Amaral et al., 2003; Keil et al., 2007; Rudrauf et al., 2008; Vuilleumier, 2005). This neurophysiological mechanism could potentially account for tradeoff effects in low-level perception triggered by unattended negative visual emotional stimuli (e.g., feaful faces, see Phelps et al., 2006; Bocanegra and Zeelenberg, 2009).

Rationale for the study

An unanswered question is whether attention selection and affective state each contribute separately to the perceptual encoding of an incoming visual stimulus in V1, or whether these two concurrent factors may show interaction effects instead. Because attentional load (Rauss et al., 2009, 2012) and emotion control (Stolarova et al., 2006) by themselves yield amplitude modulations of the C1 component during visual perception, we hypothesized a possible combined effect of the two factors influencing this early visual evoked component. More precisely, because negative affect typically leads to a narrowing of spatial attentional focus (Derryberry and Reed, 1998; Derryberry and Tucker, 1993; Easterbrook, 1959), we surmised that the transient induction of a negative affective state may alter the normal attentional filtering in V1. Therefore, we predicted that normal early load-dependent attention effects at the level of the C1 in response to peripheral, irrelevant stimuli, may be altered after the induction of state anxiety, relative to a control condition. By comparison, under positive affective state, we hypothesized that decreasing (perceptual) load at fixation ought to result in a larger C1 component in response to the exact same peripheral distractors, consistent with previous results (Rauss et al., 2009) and early attention selection models (Lavie, 2005).

To address this question, we used a standard experimental paradigm (Schwartz et al., 2005), and recorded high density VEPs to unattended peripheral distractors while parametrically manipulating perceptual load at fixation. Critically, either a negative or positive affective state was transiently induced while participants performed a demanding task at fixation, enabling us to test whether the amplitude of the C1 component generated in response to these visual peripheral distractors could be influenced concurrently by perceptual load and affective state.

Materials and methods

Participants

Twenty-five university student volunteers participated in the study (mean age = 22 years, S.D. = 2 years, 11 males, 23 right handed). Participants had normal or corrected-to-normal vision, were unaware of the purpose of the study and declared no history of psychiatric or neurological disorders. None of them had used any psychoactive medication before or during testing. The study protocol was designed and conducted in accordance with the Declaration of Helsinki and approved by the local ethical committee of Ghent University.

Stimuli and task

During a visual oddball task (standard-target proportion 4:1) participants saw at fixation a rapid serial visual presentation (RSVP) of tilted gray lines on a black background (see Fig. 1). The standard lines were always equally tilted (35° clockwise in half of the session, counterclockwise in the other half of the session, subtending 0.8° of visual angle). Randomly intermixed with the standard lines, deviant lines with a slightly different in-plane orientation were presented: participants were instructed to treat them as targets, and silently count their occurrences during the whole duration of the block (i.e., mental counting task). Participants were prompted to enter this number at the end of each block. The angular difference between standard and target stimuli was manipulated in order to obtain a parametric variation along the perceptual load dimension[1]: in the Low Load (LL) condition the difference consisted in 10° of angle (standards inclined 35°, targets inclined either 45° or 25°); in the intermediate condition (Medium Load, ML) the difference was reduced to 5° (standards inclined 35°, targets inclined either 40° or 30°). This angular difference was further reduced to 3° in the High Load condition (HL, standards inclined 35°, targets inclined either 32° or 38°). Target and standard lines were presented for 250 ms in the center of the screen, with an average ISI of 1325 ms (randomly varied between 1150 and 1500 ms). Peripheral, non predictive visual textures of horizontal line elements (8.8° × 34° of visual angle) were flashed for 250 ms in the upper visual field during the ISI. These peripheral distractors were previously associated with the generation of a conspicuous C1 component, with its main generators source-localized in V1 (Pourtois et al., 2008; Rauss et al., 2009). The peripheral textures were presented with a temporal jitter with

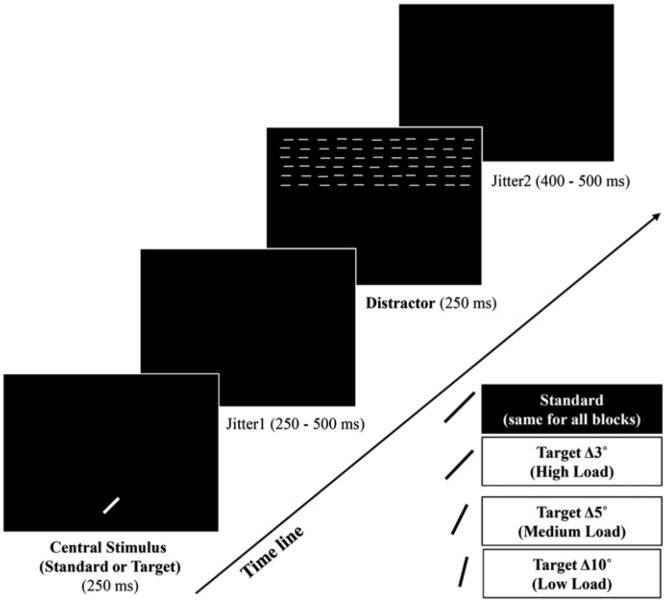

Fig. 1. Stimuli and task. Participants were instructed to attended to a rapid serial visual presentation (RSVP), consisting of small line segments shown in the center of the screen. A new small line was presented every ~1450 ms. Critically, a peripheral visual texture was flashed in the upper visual field at an unpredictable time following the presentation of the central line. Central stimuli and peripheral distractors never overlapped in space and time. The task of the participant was to (silently) detect and count the number of deviant lines during this RSVP. Peripheral distractors had to be ignored. Within a block, the ratio between standard and target orientations was 4:1. Across experimental blocks, standard orientation remained unchanged, but the angular difference between these two orientations could be large, intermediate or small, making the perceptual load of the task low (LL), medium (ML) or high (HL). Each participant performed three blocks of this task under positive affect (LL, ML and HL, in this order) and three other under negative affect (HL, ML and LL in this order). The standard line orientation (and target orientations) alternated between these two conditions, from clockwise to counterclockwise (counterbalanced across subjects).

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[1] Although our main manipulation concerns variations in the discrimination difficulty, it does not correspond to the construct of stimulus degradation *per se* (Lavie and De Fockert, 2003). Instead, it shares more similarities with the original construct of perceptual load (i. e., primarily taxing processing capacities), put forward previously (Lavie, 1995, 2005), and similarly implemented in previous studies (e.g., Barnhardt et al., 2008; Erthal et al., 2005; Handy and Mangun, 2000, experiment 1). Therefore, we label our attention manipulation *perceptual load* throughout the manuscript.

respect to the offset of the central stimuli, thus never overlapping in time with them, and they were to be ignored by the participants.

A total of 100 central stimuli were presented per block (80 standards, 20 targets), while 50 visual textures were shown (10 following a target stimulus, 40 following a standard stimulus, using a pseudo-random order). Accordingly, in only half of the trials the central stimulus was followed by a peripheral distractor. For the other half, no peripheral distractor was presented following the central stimulus (although the trial structure was temporally identical), providing a baseline condition used in some auxiliary analyses controlling for component overlap (see here below). Note that although the visual targets (small lines with deviant orientations) corresponded to perceptually different stimuli across the three load levels, both peripheral distractors and central standard stimuli remained unchanged throughout the whole experimental session (except for the clockwise/anticlockwise orientation change of the central stimuli between the two halves of the session, see procedure). This procedure allowed us to compare, at the electrophysiological level, the perceptual processing of the exact same stimuli (peripheral distractors following standard stimuli) while perceptual load at fixation was varied in a parametric fashion. The peripheral textures were presented with a vertical offset of 7.3° of visual angle above fixation during the test blocks, and randomly above or below fixation (identical distance from fixation) during two independent extra blocks, carried out at the end of the main experimental session. These blocks were used to ensure that a reliable C1 component in response to the distractors could be recorded in each and every participant, showing the expected polarity reversal depending on stimulus position in the visual field (i.e., negative amplitude for the C1 for stimuli shown in the upper visual field, but positive amplitude for stimuli shown in the lower visual field, see Clark et al., 1995; Jeffreys and Axford, 1972). Hence, these two additional blocks served as “localizer” for the C1 component. They were composed of 80 trials each (with passive viewing instructions, which emphasized fixation in the center of the screen), with an equal number of stimuli falling randomly in the upper vs. lower visual field.

Procedure

Participants were first required to sign an informed consent form, and then prepared for the EEG recording. After preparation they were positioned in a dimly lit cabin, comfortably sitting at 57 cm from a 19″ CRT screen (100 Hz refresh rate), with head motions restrained by a chinrest. Participants were then asked to perform the first 3 blocks of the mental counting task, preceded by instructions and a short practice block. No information on the initial level of difficulty was provided to the participants. Instead, we used a “cover story” during the instruction phase: participants were led to believe that the focus of the experiment was the ability to learn to process different angular orientations, and that the feedback after each block would accurately inform them about their performance. Instructions emphasized the (putative) staircase nature of the block sequence, such that participants were encouraged to believe that task difficulty experienced during block $n+1$ was solely determined by their actual performance during block n.

For half of the participants ($n=13$), each of the first three blocks was systematically followed by a Positive Feedback (PF), logically leading each time to a block of increasing difficulty (LL followed by ML, followed by HL). The feedbacks consisted in a neutral face[2] providing a message (written in a balloon). The message told the participant that his/her performance was very good, and that the (alleged) accuracy score was above average, relative to the mean performance of a group of matched participants. A scatterplot (pseudo-randomly generated), shown next to the face, showed the participant's score (in the upper part of the distribution), relative to that of the preceding participants. The feedback was presented for 20 s before the participants received instructions again about the level of task difficulty to be encountered during the following block.

The other half of the participants ($N=12$) received a different fixed order of blocks (HL, ML and LL). Each block was systematically followed by a Negative Feedback (NF), leading to an easier block in terms of task difficulty (HL followed by ML, itself followed by LL). The structure of the PFs and NFs were identical, with the exceptions that in the NF the message in the balloon stated that performance was poor, and that the accuracy score of the participant was lower than the average of the group. In line with the message, the scatterplot showed the participant's score in the lower half of the distribution. Once the three first blocks were completed, several self-report state-dependent affective measures were administered (Rossi and Pourtois, 2011). Then, participants moved to the second part of the experiment. Task instructions were similar to the ones of the first part, except that participants were told that from then on their processing ability of a different line orientation would be assessed. In detail, target and standard lines would be tilted counterclockwise if the stimuli in the first part (i.e. first three blocks) were tilted clockwise, or vice versa. After completing a new practice block, three new test blocks were presented. During this second half of the experiment, not only the line orientation, but also the feedback contingency (and fixed sequence of load levels) was counterbalanced: participants who received three PFs in the first part of the experiment now received three NFs, and symmetrically for the participants who received three NFs during the first part. In the former group, participants now started with HL (then received negative feedback), and went on with ML and finally LL. In the latter group, participants started with LL (then received positive feedback), and went on with ML and finally HL. At the end of the second series of three test blocks, affective state measures were administered a second time. The added value of this procedure is that a specific affective state (either positive or negative) may be reliably induced, depending on the valence of the feedback on task performance (Nummenmaa and Niemi, 2004). The systematic association between a given feedback valence and a fixed order of load (i.e., positive feedback with ascending load and negative feedback with descending load; counterbalanced across participants) also ensured that participants remained sufficiently motivated and attentive to the feedback information displayed during the whole experimental session. Presenting a more difficult block (i.e., higher load) after a negative feedback, or conversely an easier block (i.e., lower load) after a positive feedback, would have hampered motivation and involvement in the task. Moreover, this procedure allowed us to compare, using a within-subject design, effects of negative vs. positive affective state on task performance and electrophysiological responses to the exact same visual distractors as well as the central line stimuli.

The participants then completed two more blocks that were used as an independent localizer for the C1 component generated in response to the same peripheral distractors. These blocks were identical to the six experimental blocks, except that the central stimulus was replaced by a fixation cross and the peripheral distractors were randomly shown either in the upper or lower visual field. Participants were asked to keep fixation during these blocks (passive viewing). Finally, participants filled out additional trait-related questionnaires (i.e., STAI-T, Spielberger, 1983; BIS/BAS, Carver and White, 1994) before leaving the experimental room and receiving a complete debriefing about the goal of the study.

Affective measures

Changes in affective state induced by our feedback manipulation were monitored using a set of standard self-report measures. Two measurement moments were implemented: a first one after completing the first three blocks (with constant feedbacks, either positive or

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[2] Stimulus number NE041 or NE083 from the standardized Ekman series (Ekman and Friesen, 1976).

negative, counterbalanced across participants), and a second one after completion of the last three blocks (with constant feedbacks, and an opposite valence compared to the first three blocks).

State anxiety measure

The Dutch version of the State Anxiety sub-scale of the State-Trait Anxiety Inventory (STAI-S, Spielberger, 1983) was administered to the participants.

Mood Visual Analog Scales (VASs)

Since our study also included induction of a positive mood (or presumably, a down-regulation of stress levels induced by the task demands through the presentation of positive feedback), seven 10 cm horizontal VASs were included in the affective state assessments, in order to provide a more balanced estimate of affect (taking into account changes not only for negative affect, but also positive affect). The anchors for the VASs (the Dutch translation for the terms '*Tired*', '*Energetic*', '*Angry*', '*Tense*', '*Depressed*', '*Satisfied*', and '*Happy*') were selected from the sub-scales of the Profile of Mood States questionnaire (POMS, McNair et al., 1992), with the integration of VASs for satisfaction and happiness. As it is common use for the POMS (Rossi and Pourtois, 2011), a compound measure of affective state was calculated by adding up the scores of the seven items (the two positive affect items were reverse-scored): the compound score ranges therefore from a minimum of 0 (minimum level of negative affect) to a maximum of 70 (maximum level of negative affect).

Electrophysiological data recording

EEG was continuously recorded from 128 Ag/AgCl electrodes evenly distributed over the scalp surface using an elastic cap (Biosemi Active Two System, http://www.biosemi.com). Signals were online referenced to the CMS–DRL ground (driving the average potential across the montage as close as possible to the amplifier zero), and digitized at 512 Hz. Vertical and horizontal oculograms were monitored through bipolar electrodes positioned on the outer canthi of each eye and above and below the left eye.

Two bipolar electrodes were also applied to the volar surfaces of the medial phalanges of the left hand in order to record skin conductance levels (SCL) throughout the whole session. Participants were instructed to comfortably lay their forearms on the table and asked not to move during the experimental blocks.

Data reduction and analysis

ERP waveforms obtained from the two localizer blocks and the six test blocks were computed separately, using Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany). EEG signals were referenced offline to the linked mastoids and band-pass filtered between 0.016 and 70 Hz; a notch-filter (50 Hz) was applied. EEG signals were segmented relative to the onset of either the central stimulus or the peripheral distractor, using a 100 ms pre-stimulus interval and a 800 ms post-stimulus interval. In order to avoid possible contamination from mental counting operations (e.g., updating of working memory) on the perceptual processing of the peripheral distractors, only textures following standard (i.e., non-target) central stimuli were included in the averages. Eye-blink artifacts were detected and corrected automatically by means of the Gratton et al. (1983) algorithm. Individual epochs were baseline-corrected using the 100 ms pre-stimulus onset interval, and all epochs affected by residual artifacts were semi-automatically rejected on the basis of an absolute voltage criterion of ±75 μV difference, relative to the baseline. This procedure led to an average rejection rate of 7.4% of the trials, balanced between the two halves of the experiment (i.e. positive vs. negative affect induction). For central stimuli, rejection rate reached 7.9% in the positive emotion condition and 7.0% in the negative emotion condition ($t_{24}=0.77$, $P=.44$). Likewise, for peripheral distracters, rejection was 7.3% for positive and 7.6% for negative ($t_{24}=0.26$, $P=.80$). Individual ERP averages for central targets and peripheral distractors were computed for each subject separately as a function of load level (HL, ML, LL) and feedback condition (PF, NF), and subsequently grand-average ERP waveforms for each of these six conditions were obtained by averaging data across participants. For the localizer blocks, peripheral distractors presented either below or above fixation were analyzed and averaged separately, following the same procedure as described here above (mean rejection rate for trials in the upper visual field: 8.3%; lower visual field: 9.4%; $t_{24}=1.44$, $P=.16$). Based on previous results (Rauss et al., 2009, 2012) and visual inspection of the grand average data, the visual C1 in response to the peripheral distractors during the six test blocks was semi-automatically identified as the most negative peak present in the stimulus-locked ERPs between 70 and 110 ms after stimulus onset. Since no differences in peak latency were evident across load conditions in the grand-averaged data (consistent with previous findings, see Rauss et al., 2009, 2012), we primarily focused our analyses on the peak amplitude of the C1 component. Based on topographic properties of the grand averaged data (highly consistent between localizer runs and test blocks; see Figs. 4–6), the C1 was primarily scored at the midline leads A4, A19, A20 and A21 (where A19 actually corresponds to electrode Pz in the International extended 10–20 System, and these four electrodes span from centro-parietal A4/CPPz to more occipital positions A20/PPOz and A21/POz, along the midline, see Fig. 6). Moreover, in order to rule out that the observed C1 modulations by load and affect may be due to a partially overlapping contribution of the onset phase and rise of the occipital midline P1 (P1m, see Fu et al., 2009; see also Handy et al., 2001), we also analyzed the peak amplitude of this extrastriate visual component as a function of Load and Affect. The P1m had a more occipital scalp distribution than the C1 (showing a typical occipito-parietal distribution along the midline, see Figs. 4C and F), and accordingly, the amplitude of this component was measured at parieto-occipital midline electrodes A20, A21, A22, A23 (with A20 corresponding to POz and A23 to Oz, see Fig. 6).

Given that we used short tilted line segments as central task-relevant stimuli, these visual events elicited a clear P300 component, while the magnitude of the preceding lateral occipital P1 and N1 components remained negligible (see Fig. 3A). Accordingly, we analyzed and reported mainly amplitude variation of the P300 component for these central task-relevant stimuli.[3] The P300 in response to standards and targets belonging to different load levels in each of the two affective conditions was identified on the basis of polarity and scalp distribution properties, in line with previous ERP studies (Kim et al., 2008; McCarthy and Donchin, 1981; Sawaki and Katayama, 2007). The component was scored as the mean amplitude of the ERP response between 500 and 700 ms after stimulus onset, at centro-parietal–occipital leads (A4/CPPz, A19/Pz, A20/PPOz and A21/POz) along the midline. C1 peak scores and P300 mean amplitude scores were analyzed separately by means of mixed-model analyses of variance (ANOVAs), with Load (LL, ML, HL), Affective Condition (NF, PF) and Lead (A4, A19, A20, A21) as within subjects factors, and Group (PF first, NF first) as between subjects factor. Post-hoc comparisons were performed using two-tailed paired samples T-tests. Control analyses were also run for both components as a function of block order (see Results section). Because we used a RSVP, we also run a control analysis to ascertain that the C1 component generated by the peripheral distractors was not systematically influenced by residual ERPs from the preceding central stimuli. For this purpose, we

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[3] Additional statistical analyses performed on the residual P1 and N1 components (time-locked to the onset of the task-relevant central stimuli, measured as mean amplitude of the ERP response at a cluster of lateral occipital leads) did not reveal any significant effect of affect or interaction between load and affect.

used a standard correction, namely the no-stim technique (Talsma and Woldorff, 2005). ERP waveforms computed for epochs where no peripheral stimulus was presented (i.e. overlap alone; 50% of the trials) were subtracted from ERP waveforms where a peripheral stimulus was presented (i.e. peripheral stimulus-specific ERP activity + overlap; 50% of the trials). As a result, 'overlap-free' stimulus-locked ERP waveforms, including the C1, were obtained and later compared across affective states and load conditions (LL, ML and HL).

We used the bipolar vertical electro-oculogram (VEOG), continuously recorded during the whole experiment, to quantify the spontaneous eye-blink rate, used as an indirect measure of anxiety (Karson, 1983; Ponder and Kennedy, 1927). Eye-blinks were automatically detected using the Brain-Vision Analyzer ocular correction algorithm during each of the six test blocks and analyzed using a 3×2 repeated measures ANOVA with Affective Condition (NF, PF) and Order (First block, Second Block, Third Block) as within-subjects factors. Note that the factor Order was selected in this statistical analysis (instead of the factor Load) because our primary goal was to verify whether the valence of the feedback could have a systematic influence on the spontaneous blink rate recorded during the immediately following block (i.e., we expected increases in blink rate and hence anxiety for blocks 2 and 3 in the NF condition regardless of load, but no similar effect for blocks 2 and 3 in the PF condition).

Changes in affective state induced by the feedback manipulation were also verified by comparing directly the self-report scores obtained for the two measurement points (i.e. after the first three blocks, and a second time after the last three blocks) in the STAI-S and in the compound VAS. Because we predicted increased levels of state anxiety and negative affect following NFs, one-tailed paired samples T tests were used. In order to further explore the exact nature of the discrete affective state induced by our manipulation, we also carried out an analysis comparing the pre-post scores separately for the anxiety-present and anxiety-absent items of the STAI-S (Spielberger, 1983).

In order to compare levels of peripheral arousal during the positive and negative halves of the experiment, the continuously recorded SCL signals were segmented based on the onset of each of the six experimental blocks, in epochs of 143 s. The average SCL values in the time-window ranging from 0 to 143 s (end of the block) were extracted and range-normalized following a standard procedure (Lykken and Venables, 1971). The normalized average SCL values obtained for the three blocks followed by PFs were averaged together, as were the values obtained for the three blocks followed by NFs. These two scores were then compared using a paired sample T-test (two-tailed). Furthermore, we also analyzed more phasic changes in SCL in response to the six feedbacks (three positive, three negative). These electrodermal response values were calculated as the maximum signal amplitude during the feedback presentation window (0–20 s), corrected for the minimum amplitude recorded during 10 s prior to feedback presentation. We then range-normalized these difference scores (Lykken and Venables, 1971) and entered the 6 values in a repeated measures ANOVA with condition (Positive, Negative) and order (first, second and third feedback) as factors.

Accuracy during the main task was computed by calculating for each subject the difference between the number reported at the end of each block and the correct number of deviant tilted lines (= 20). We calculated for each participant and each block separately the absolute deviation from the correct response (computed as |Correct Response minus Actual Response|) and submitted these values to a mixed model ANOVA with Load (LL, ML, HL) and Affective Condition (NF, PF) as within subjects factors, and Group (either PFs or NFs first) as between subjects factor.

Since the between subjects factor Group did not yield any significant effect or interaction with any of the other factors included in our experimental design (neither in the ERP results, nor in the behavioral ones), the data of the two groups were collapsed in the statistical analyses. A Greenhouse–Geisser correction was applied when sphericity was violated, therefore significant results are reported with uncorrected degrees of freedom but corrected p values.

Results

Affective state

STAI-S scores were substantially higher after NFs (M = 36, S.D. 8.9) than PFs (M = 32, S.D. 7.9, $t_{24} = -3.932$, $P < 0.0001$) suggesting increased state anxiety following NFs. This change was equally evidenced for the anxiety-absent items ($t_{24} = 3.76$, $p < .001$) and the anxiety-present items ($t_{24} = 3.25$, $p < .005$), consistent with the idea that the feedback manipulation did not lead to a pure increase of state anxiety per se, but probably to an augmented negative affective state. Likewise, the compound VAS score obtained after combining the seven subscales showed a significant increase in negative affect after NFs (M = 20.73, S.D. 9.61), as compared to the scores obtained after PFs (M = 17.10, S.D. 6.98), $t_{24} = -2.785$, $P < 0.01$ (see Fig. 2, panel A).

The ANOVA performed on the spontaneous eye-blink rate corroborated these findings (subjective self-report measures) and suggested increased levels of tension or anxiety following the presentation of NFs, as evidenced by a significant interaction between Affective Condition and Order ($F_{2,48} = 6.01$, $P < 0.01$). Post-hoc comparisons using two-tailed paired-samples T tests revealed a significant increase in blink rate from the first (M = 25 blinks) either to the second (M = 32 blinks) or third block (M = 32 blinks) in the NF condition (block 1 vs. 2: $t_{24} = -3.03$, $P < 0.005$; block 1 vs. 3: $t_{24} = -2.69$, $P < 0.05$). Blink rate did not differ significantly between blocks 2 and 3 ($t_{24} = 0.29$, $P > 0.7$). None of the planned comparisons reached significance in the PF condition (all $Ts < 0.3$, all $Ps > 0.7$). These results suggest increased and sustained levels of anxiety, selectively following NFs, and as such, are in line with the results obtained for the self-report measures (cf. Figs. 2A and B).

Finally, we obtained additional evidence indicating that affective changes produced by the feedback likely concerned negative affect or state anxiety, but not simply peripheral (autonomic) arousal. The SCL continuously recorded while the participants performed the task did not significantly differ between the two affective conditions ($t_{24} = 1.07$, $P = 0.30$ for the normalized data; $t_{24} = 1.16$, $P = 0.26$ for the non-normalized data), suggesting that (peripheral) arousal per se did not account for the observed differences in affective state produced by our feedback manipulation (see Fig. 2C). In addition, although evaluative feedback stimuli clearly elicited phasic changes in SCL, the ANOVA carried out on these normalized values did not reveal any significant effect of affective state or order (all $Fs < .48$). Combined together, these non-significant results for the SCL suggest that our participants did not undergo systematic changes in peripheral arousal during exposure to the evaluative performance feedbacks (phasic component) or during the execution of that task itself (tonic component).

Behavioral performance

Results obtained during the main EEG experiment confirmed that the load manipulation was efficient and produced, as expected, a decreased performance when increasing perceptual load at fixation (see Table 1). However, this effect was similar for the positive and negative affective state condition. The ANOVA carried out on the accuracy scores revealed a significant main effect of Load ($F_{2,48} = 11.90$, $P < 0.0001$), but no significant effect of Affective Condition or interaction between these two experimental factors (all $Fs < 1.09$, all $Ps > 0.3$). Post-hoc paired samples T-tests showed that accuracy was significantly higher in the LL condition as compared

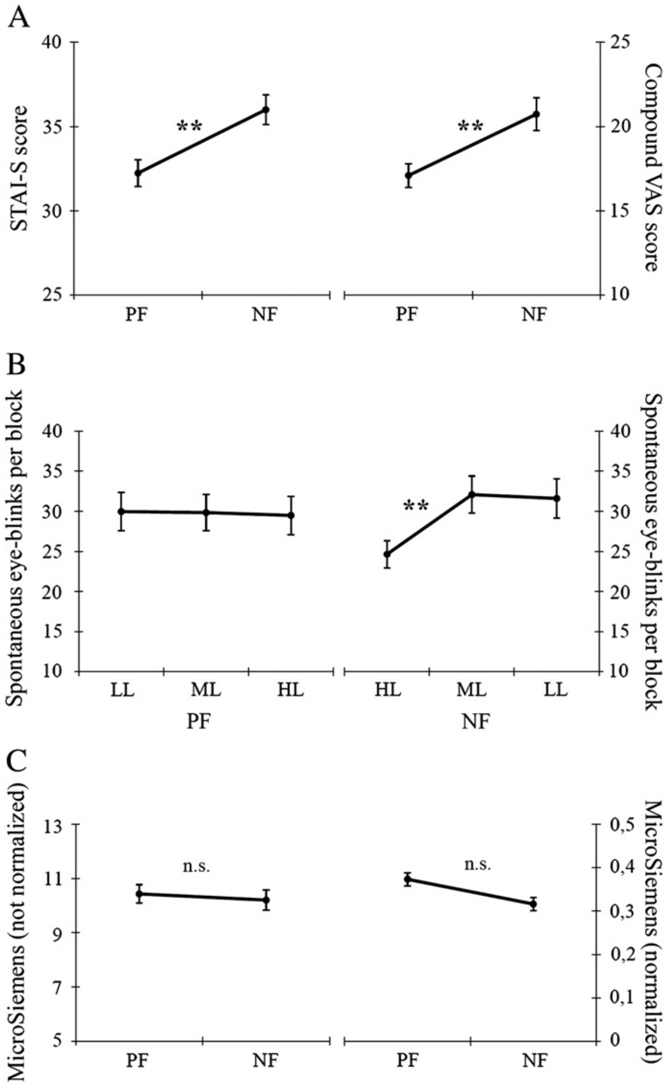

Fig. 2. Results of self-report and psychophysiological (peripheral) measurements (the symbol ** indicates a significant effect with P<0.01, and error bars represent 1 S.E.M.). (A) Left panel: the STAI-S scores, providing an estimate of the state-dependent level of anxiety, reliably increased after receiving negative, compared to positive, feedbacks. Right panel: the compound VAS scores substantially increased in the negative, relative to the positive affect condition. (B) Left panel: spontaneous eye-blink rates recorded during the experimental blocks associated with positive feedbacks. No change in the eye-blink rate was observed. Right panel: spontaneous eye-blink rates recorded during the blocks associated with negative feedbacks. A sharp and sustained increase of the spontaneous blink rate was evidenced following the presentation of the first negative feedback. (C) Left panel: Comparison between the mean skin conductance level (SCL) values (not range-normalized) recorded during the induction of positive vs. negative affect. No difference across the two emotion conditions was observed. Right panel: Results obtained with the range-normalized SCL values corroborated this conclusion. (PF: Positive Feedback; NF: Negative Feedback; LL: Low Load; ML: Medium Load; HL: High Load).

to either the ML ($t_{24}=-1.99$, P<0.05, one tailed) or the HL condition ($t_{24}=-4.72$, P<0.00001, one tailed); accuracy was also higher in the ML condition as compared to the HL condition ($t_{24}=-3.22$, P<0.01, one tailed). Average error scores were 4.5 (S.D. 4.6) for LL, 6.5 (S.D. 5.3) for ML and 8.8 (S.D. 4.6) for HL. These results suggest that changes in perceptual load reliably led to changes in behavioral performance, in a predictive way (see also Barnhardt et al., 2008; Erthal et al., 2005; Lavie, 1995; Rauss et al., 2009, 2012; Schwartz et al., 2005). Importantly, this effect was the same for the two affective states conditions, and behavioral performance in the HL condition was still acceptable.

Table 1
Behavioral performance in the mental counting task for Low, Medium and High Load blocks, separately for positive and negative affective conditions. Values correspond to the absolute deviation from the correct response and corresponding standard deviations (S.D.).

	Low Load	Medium Load	High Load
Positive feedback condition	4.5 (S.D. 5.6)	7.7 (S.D. 8.3)	9.5 (S.D. 7.1)
Negative feedback condition	4.5 (S.D. 6.7)	5.2 (S.D. 4.5)	8.0 (S.D. 4.6)

ERP results

ERPs for central target stimuli

The ANOVA performed on the mean amplitude of the P300 in response to the central targets revealed a significant main effect of Load ($F_{2,48}=44.99$, P<0.0001), but no other significant effect (all Fs<1.15, all Ps>0.3). Post-hoc paired samples T tests showed that the P300 for target stimuli in the LL condition had a significantly larger amplitude than the targets either in the ML condition ($t_{24}=5.61$, P<0.0001, two tailed) or in the HL condition ($t_{24}=7.37$, P<0.0001, two tailed). Additionally, the P300 amplitude in the ML condition had a significantly larger size than in the HL condition ($t_{24}=6.32$, P<0.0001, two tailed). These results confirmed that target identification (and presumably covert detection) was affected by the load manipulation in a predictive way, with easier detections during the LL (as reflected by a larger P300 component) compared to the ML condition, this latter condition being easier than the HL condition (see Figs. 3A and C, upper panel). These results are also consistent with previous ERP results, reporting decreased P300 amplitudes with increased perceptual load or task difficulty (Kim et al., 2008; McCarthy and Donchin, 1981; Sawaki and Katayama, 2007; for a review, Kok, 2001).[4]

ERPs for central standard stimuli

The centrally presented standard stimuli did not elicit a clear P300, as compared to the target stimuli (as it is evident in Figs. 3B and C, lower panel). Nonetheless, to assess whether our affective state manipulation might influence the processing of these stimuli, we analyzed the mean amplitude of the ERPs in response to central standards across load and affective conditions at the same leads and in the same time window as we used for the target stimuli (500–700 ms post-stimulus onset; electrodes A4/CCPz, A19/Pz, A20/PPOz and A21/POz). The ANOVA showed a significant main effect of Load ($F_{2,48}=8.54$, P<0.01), and a non-significant trend for the factor Lead ($F_{3,72}=3.36$, P=0.07). Paired T-tests indicated that the slow positive wave was larger under LL as compared to ML ($t_{24}=3.96$, P<0.0001, two tailed) and to HL ($t_{24}=2.71$, P<0.05, two tailed). No

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[4] Because the task consisted in a mental counting task and an overt response was required only at the end of each block, we could not retrospectively isolate trials corresponding to seen targets, as opposed to (presumably) missed targets. Therefore, this reported significant effect for the P300 component might tentatively be explained by the inclusion of more misses in the HL compared to the ML condition (and ML compared to LL), rather than a genuine change in perceptual load across these conditions. However, to address this point, we performed a control analysis and modeled the hypothetical 'dilution' of the P300 component when increasing load. Since the hypothetical SNR values (obtained by dividing the number of correctly identified targets by the number of missed targets in the behavioral data) were different across conditions (1.22 for HL, 2.33 for ML and 3 for LL), we artificially matched the SNR level for the ERP data across load conditions by adding to the target-locked grand averages (in ML and LL) a proportion of standard stimuli (which presumably should not elicit any reliable P300 component, and therefore may be used to "simulate" ERP activity corresponding to missed targets in these conditions). As a result of this control analysis, the SNR level of ML and LL ERP averages were reduced to the one corresponding to HL (i.e., 1.22). If the reported modulation of the P300 was accounted for by the proportion of perceived vs. missed targets rather than perceptual load, then this analysis should lead to the same P300 component across the three load levels. However, this control analysis confirmed a strong load-dependent variation of the P300 (LL>ML>HL; all $T_{23}>4.61$, all Ps<.001), despite a balanced SNR level across these three conditions.

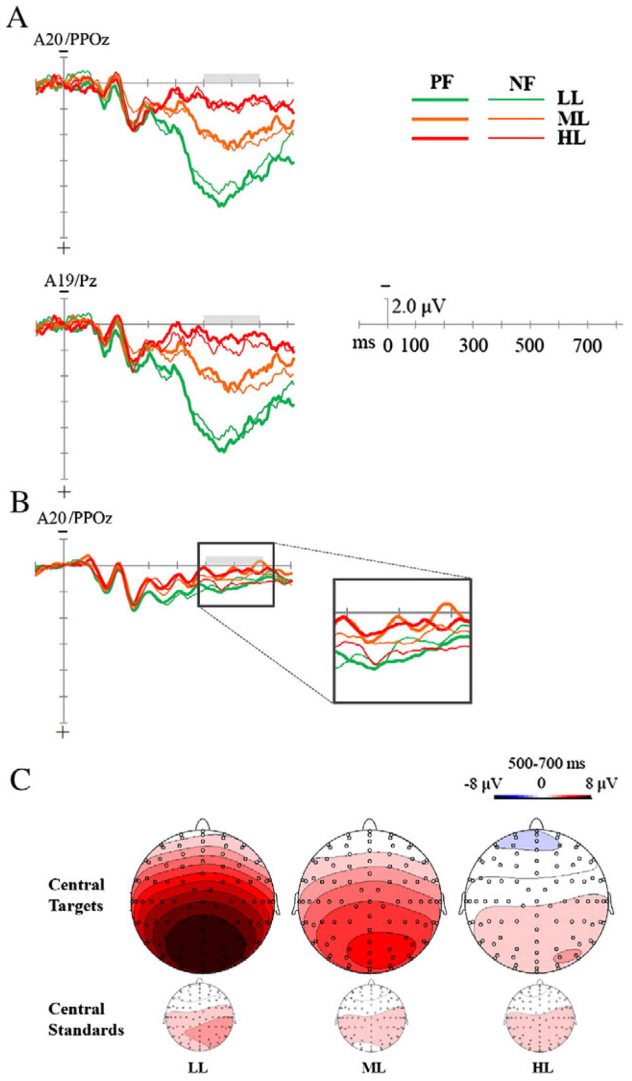

Fig. 3. (A) Grand average ERPs to central target lines at two representative occipito-parietal electrode positions along the midline. A reliable parietal P3 component was evidenced, with a mean latency of ~550 ms following stimulus onset. This decision-related ERP component substantially varied in amplitude with perceptual load, being larger for LL (green), intermediate for ML (orange) and smallest for HL (red), consistent with a parametric modulation of target detection brain processes with perceptual load. This systematic load-dependent modulation of the P3 component was similar for the positive and negative affective state conditions (thick vs. thin lines). The shaded area on the horizontal axis shows the interval (500–700 ms post-target onset) used to compute the mean amplitude of the P3. (B) Grand average ERPs to central standard lines at a representative parietal electrode (PPOz). No clear P300 component was generated in response to these attended central stimuli (compare with Fig. 3A and P300 elicited for target stimuli). Nevertheless, an analysis performed on the mean amplitude of this residual/slow wave in the same time-window (i.e. 500–700 ms post-stimulus onset; see inset in the Fig. 3B) showed a significant main effect of Load, but no interactions with Affect (see Results section for exact values). (C) Voltage maps (horizontal view) of the P3 component, separately for the three load levels, showing that the amplitude of this centro-parietal ERP activity linearly decreased with increased perceptual load, while the configuration of the electric field remained unaffected by these changes. (A-Right panel) Grand average ERPs to central standard lines recorded at the midline occipito-parietal electrode A19. The comparison with the target-locked ERPs (see left panel) confirmed that the P3 component was mostly sensitive to target processing and the covert detection of lines with deviant orientations (see Materials and methods). (PF: Positive Feedback; NF: Negative Feedback; LL: Low Load; ML: Medium Load; HL: High Load).

differences were observed between the ML and the HL condition ($t_{24} = -1.39$, $P > 0.17$, two tailed). The main effect of Affective Condition was not significant ($F_{1,24} = 0.98$, $P = 0.33$), nor was there a significant interaction between Load and Affect, or Load, affect and Lead (all $Ps > 0.15$).

ERPs for peripheral distractors: C1

The ANOVA performed on the mean amplitude of the C1 generated in response to the peripheral distractors showed a significant main effect of Load ($F_{2,48} = 4.80$, $P < 0.05$), but more importantly, this load-dependent effect did significantly interact with the Affective Condition ($F_{2,48} = 7.94$, $P < 0.005$). Post-hoc paired samples T tests revealed that the amplitude of the C1 varied, in a predictive way, with the load level (i.e. lower amplitude during HL than LL; see also Rauss et al., 2009) during the positive affective state condition, but that this effect was merely absent during the negative affective state condition (see Fig. 4ABC for the Positive Feedback condition, and Fig. 4DEF for the Negative Feedback condition). For the positive affect condition, larger C1 amplitudes were found in the LL condition as compared either to the ML ($t_{24} = -3.16$, $P < 0.005$, two tailed) or the HL condition ($t_{24} = -4.95$, $P < 0.001$, two tailed). The C1 amplitude was similar between the ML and HL condition ($t_{24} = -0.951$, $P > 0.4$, two tailed). For the negative affect condition, no significant modulation of the C1 as a function of load was observed (all $ts < |1.6|$, all $Ps > 0.1$).

A detailed inspection of the ERP data generated in response to these peripheral visual distractors during the positive affective state condition suggested that before the peak of the C1, an even earlier (and unexpected) effect of load (50–70 ms post-stimulus onset) was already present. This effect led to a more negative baseline amplitude for the LL relative to HL condition, although no pre-stimulus ERP difference could be detected between these conditions (see Fig. 4ABC), suggesting that the reported C1 change as a function of load and affect was not simply explained by unbalanced baselines across conditions. Moreover, no such modulatory effect of load was observed during the same pre-C1 interval for the negative affective state condition (see Fig. 4DEF). We performed additional statistical analyses to assess whether the significant interaction effect between load and affect found at the level of the C1 (peak amplitudes) might be contaminated by this earlier effect occurring during the onset phase of the C1. First, we extracted the mean amplitude of this baseline post-stimulus activity (computed from stimulus onset until 70 ms following stimulus onset) and assessed whether a similar interaction effect was present during this pre-C1 time interval. The analysis failed to reveal any significant interaction effect between load and affect for this pre-C1 activity ($F_{2,48} = 2.38$, $P = 0.10$). More importantly, we then subtracted for each participant and condition separately, the mean amplitude values during the interval 0–70 ms post-stimulus onset from the original C1 peak amplitude values and eventually submitted these corrected C1 amplitude values to the same ANOVA as used in the main analysis. This control analysis confirmed a significant Load × Affective condition interaction ($F_{2,48} = 3.25$, $P < 0.05$), suggesting that amplitude variations of the C1 component with load and affect could not solely be accounted for by this unexpected pre-C1 variation. Using these conservative corrected peak values, this analysis confirmed a substantially larger C1 amplitude during LL compared to either ML ($t_{24} = -2.35$, $P < 0.05$, two tailed) or HL ($t_{24} = -3.09$, $P < 0.005$, two tailed) during positive affective state, but no significant and comparable effect of load on the amplitude of the C1 during negative affective state (all $Ps > 0.23$). Therefore, this control analysis confirmed that effects of perceptual load and affective state truly influenced the amplitude of the C1 component, and they could not easily be explained by changes in the baseline ERP activity following stimulus onset, but preceding the onset of this retinotopic component.

To exclude the possibility that uncontrolled pre-C1 or pre-stimulus onset variations (potentially triggered by the preceding central and task-relevant stimulus) could account for the observed C1 amplitude variations, we also used another conservative data analysis suited to remove possible residual ERP effects from the preceding stimulus (no-stim approach, see Materials and methods section above). Noteworthy, the repeated measure ANOVA carried out on the C1 amplitude values extracted from these “overlap-free” waveforms confirmed a significant interaction effect between Load and Affect ($F_{2,48}=3.59$, $P<0.05$). Follow-up pairwise comparisons confirmed a significantly larger C1 response during LL (LL: −6,47 μV) compared to either ML (−5,09 μV, $t_{24}=-2.21$, $P<0.05$, two tailed) or HL (−4,73 μV, $t_{24}=-3.61$, $P<0.005$, two tailed) during positive affective state, but no significant effect of load on this early component during negative affective state (LL: −4,72 μV; ML: −5,04 μV; HL: −5,05 μV; all $Ps>0.53$).

Although these results clearly pointed to a joint effect of load and affect on the earliest stage of sensory stimulus processing in V1, yet an additional (third) control analysis was run to ascertain that perceptual load and affect state each had a clear effect on the amplitude of the C1. Given the specifics of our experimental design,

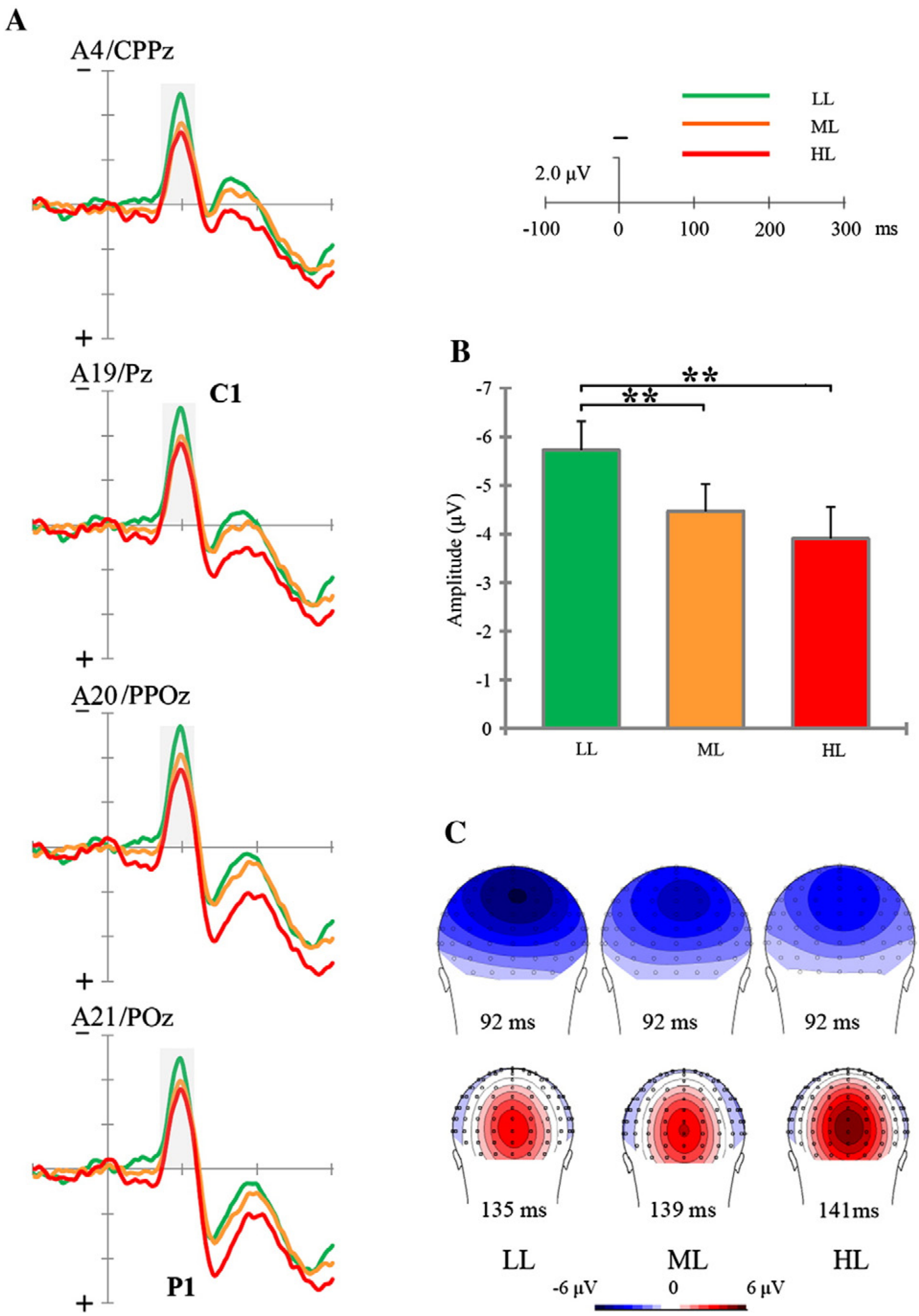

Fig. 4. Grand average ERPs to peripheral distractors at four different occipito-parietal electrode positions along the midline, either in the positive (A, B, C) or in the negative (D, E, F) affective state condition. (A) A conspicuous negative C1 component peaked ~92 ms following stimulus onset over occipito-parietal leads. Increasing perceptual load at fixation (HL) resulted in a significantly lower C1 for peripheral distractors, relative to either ML or LL, as became also evident when computing the mean amplitude (error bars indicate 1 S.E.M) of the C1 across these four electrode positions (B; the symbol ** indicates a significant effect with $P<0.01$). Before the C1 peak, an earlier effect of load arose ~50–70 ms post-stimulus onset, but this effect did not account for the changes found at the peak amplitude of the C1 as a function of perceptual load (see Results). (C) The voltage maps (back view) extracted at the C1 and P1m peak latencies confirmed that the scalp distribution of both components were stable across the three load levels; only the strength of these early VEPs varied with perceptual load. (D) Although a very similar C1 component was clearly generated to peripheral distractors under negative affective state, its amplitude did not vary as a function of perceptual load changes. (E) Examining the mean amplitude (error bars indicate 1 S.E.M) of the C1 across these four electrode positions confirmed that it did not change with perceptual load. (F) The configuration of the electric field (voltage map) corresponding to the C1 and P1m was stable and comparable across the three perceptual load conditions. (LL: Low Load; ML: Medium Load; HL: High Load).

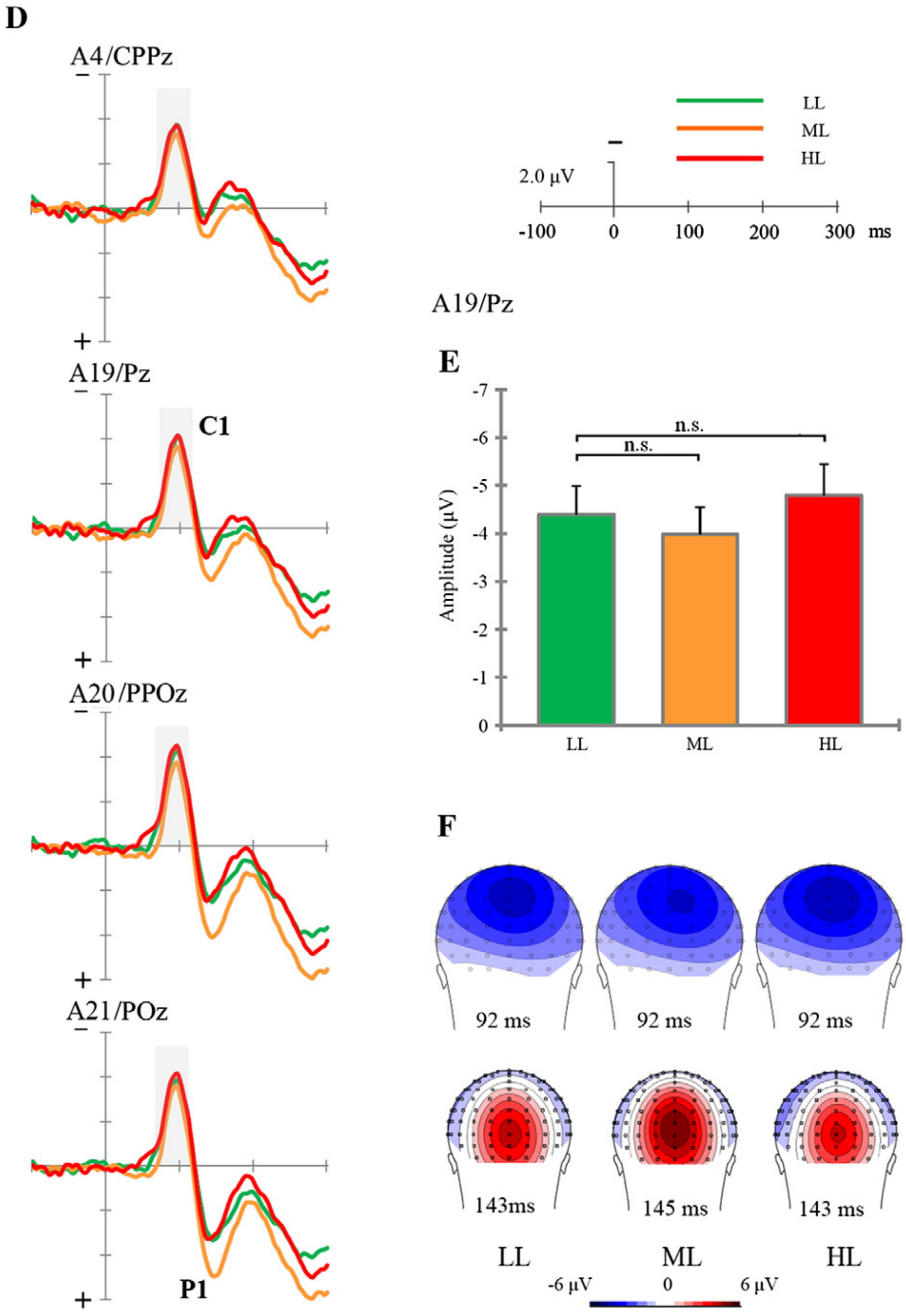

Fig. 4 (*continued*).

we assumed that during the very first block of each half of the experiment (see procedure here above), no affective state was transiently induced yet, providing a correct baseline to study pure effects of load (LL vs. HL). Hence, we extracted the amplitude of the C1 in the overlap-free waveforms during the first experimental block of each condition and compared the size of this component for LL vs. HL blocks. We reasoned that this comparison should reveal a pure effect of load on the C1, with this component being larger for LL relative to HL (see also Rauss et al., 2009). Results of this auxiliary analysis, run on the overlap-free C1 amplitudes, corroborate this conclusion (see Fig. 5, left panel). C1 amplitudes were compared using a repeated measures ANOVA with Lead and Load as factors. This analysis revealed a significant main effect of Load ($F_{1,24}=4.93$, $P<0.05$), with a larger early retinotopic component for LL(mean −6.47 μV, S. D. 3.1 μV) compared to HL (mean −5.01 μV, S. D. 3.2 μV), when no affect had been induced yet. However, we hypothesized that this significant effect of load observed on the corrected C1 amplitudes would disappear once a negative affective state would have been induced, if affect truly influenced early sensory processing of peripheral distractors in V1. Consistent with this prediction, the same repeated measures ANOVA performed on the C1 data recorded during the last block of each staircase (also corrected for potential component overlap, see Fig. 5, right panel), hence once affect had reliably been modulated (see also behavioral and psychophysiological results here above), failed to show any significant effect of Load ($F_{1,24}=0.01$, $P=0.98$), indicated by a similar C1 component for LL (mean −4.72 μV, S.D. 2.76 μV) and HL (mean −4.73 μV, S.D. 2.76 μV). Altogether, the results of these control analyses converge and confirmed (i) a normal effect of load at the level of the C1 (with larger amplitudes for LL than HL) when no affective state had been

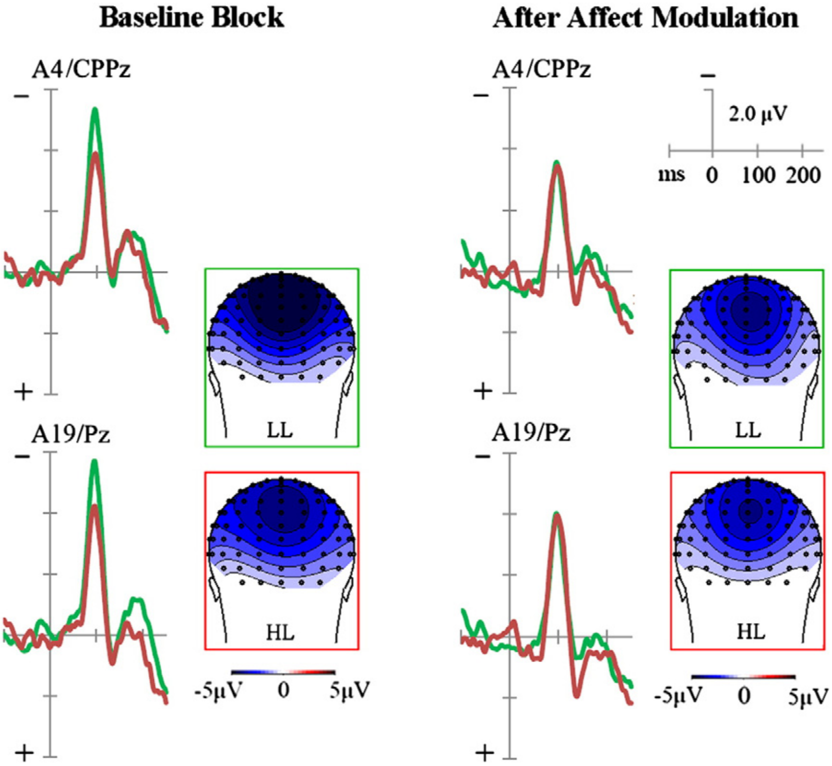

Fig. 5. Grand average overlap-free ERPs (see methods) at two representative occipito-parietal electrode positions along the midline in response to peripheral distractors, separately for each load level (Green = LL; Red = HL). The corresponding voltage maps computed for the overlap-free C1 peak (92 ms) are also shown. Left panel: grand average overlap-free ERPs and corresponding C1 voltage maps, at baseline (Block 1 of each staircase, when no reliable change in affective state had occurred yet). This analysis confirmed a clear effect of load (HL<LL) for the C1 component at baseline. Right panel: same results as for the left panel, but for the overlap-free ERP data recorded during the last block of each staircase, hence once affective state had been modulated. The significant effect of load for the C1 present at baseline (see results) was completely abolished once (either positive or negative) affect had been induced, confirming that the C1 component was comparably sensitive to load and affect.

induced yet; (ii) once (either positive or negative) affective state had been induced, this normal load-dependent attentional filtering effect was abolished.[5]

ERPs for peripheral distractors: P1

Immediately following the C1, we also detected a smaller but clear positive deflection (see Figs. 4–6), centered over occipital midline leads, showing no change in topographical distribution between the main task and the localizer runs (see Figs. 4C–F and 6). The electrophysiological properties of this component were consistent with a midline-distributed P1 (P1m, Handy et al., 2001; Fu et al., 2009, 2010), peaking between 110 and 150 ms following stimulus onset. Because of the close temporal proximity between the peak of the C1 and the rise of the extrastriate P1m, we performed a thorough analysis of the P1m component to ensure that changes in the C1 as a function of load and affect (see here above) were not accounted for by a partially overlapping P1m effects. The ANOVA performed on the peak amplitude values of the P1m revealed significant main effects of Lead ($F_{3,72} = 8.36$, $P < 0.01$) and Load ($F_{2,48} = 3.82$, $P < 0.05$). Regarding the effect of Lead (all pairwise comparisons across Leads $t_{24} > |2.41|$, all $p < .05$), the P1m had the smallest amplitude at the most parietal electrode location A20/PPOz (4.28 µV, S.D. 3.58 µV), but its amplitude increased linearly when moving towards more occipital locations, reaching its maximum amplitude at the most occipital lead included in the analysis, A23/Oz (4.60 µV, S.D. 3.44 µV). This effect is consistent with the scalp distribution of the P1m, which is markedly different relative to that of the C1 (see Fig. 4; see also Handy et al., 2001, who scored the amplitude of the P1m response to irrelevant probes centered on the vertical meridian at POz and Oz). Load also reliably influenced the amplitude of the P1m, indicated by larger P1m magnitudes when Load increased (LL: 4.64 µV, S.D. 2.56 µV; ML: 5.49 µV, S.D. 3.50 µV; HL: 5.45 µV, S.D. 3.58 µV). Interestingly, a significant interaction between Load and Affect ($F_{2,48} = 7.07$, $P < 0.01$) was also evidenced in this analysis, although this interaction effect was clearly different compared to the significant interaction effect between load and affect found for the preceding C1 component. A significantly larger P1 was elicited under ML in the negative affect condition (PF: 4.83 µV, S.D. 3.68 µV; NF: 6.13 µV, S.D. 3.69 µV; $t_{24} = -2.81$, $P < .01$), while this component reached its maximum amplitude in the HL condition when positive affect was induced (PF: 5.97 µV, S.D. 4.01 µV; NF: 4.92 µV, S.D. 3.47 µV; $t_{24} = 2.40$, $P < .05$). No significant effect of affect was evidenced for the LL condition. Altogether, these additional results for the P1m suggest that amplitude variations of this extrastriate component likely reflect another attention mechanism active during sensory stimulus processing, relative to the C1.

ERPs during the independent localizer run

As can be seen in Fig. 6, results from the localizer run confirmed a prominent C1 response generated in response to the distractor stimuli presented during passive viewing: the expected polarity reversal was clearly observed as a function of the spatial position of the peripheral texture in this visual field, with a negative C1 for upper visual field presentation and a positive C1 for lower visual field presentation. This localizer run was mainly introduced in order to provide

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[5] A similar control analysis of variance (with Lead and Load as factors) performed on the P300 mean amplitudes in response to central target stimuli revealed clear effects of Load, both at baseline (i.e., before affect induction: $F_{1,24} = 41.38$, $P < 0.0001$) and after affect induction ($F_{1,24} = 38.43$, $P < 0.0001$). This result confirmed that state anxiety induction selectively affected brain responses in V1 to peripheral distractors, while it did not reliably influence the load-dependent processing of central target stimuli.

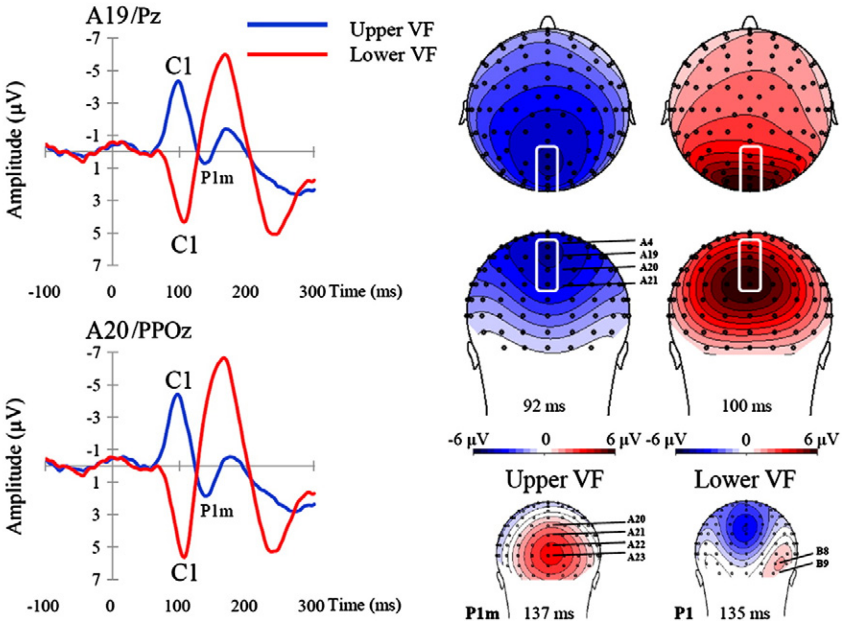

Fig. 6. Grand average ERPs at two different occipito-parietal electrode positions along the midline to peripheral distractors shown either in the upper or lower visual field during the independent "localizer" run. A conspicuous C1 component was clearly recorded ~100 ms following the presentation of the peripheral distractor over occipito-parietal leads, whose amplitude and polarity reversed as a function of the position of the stimulus in the visual field (i.e., negative for upper visual field and positive for lower visual field presentations), consistent with the electrophysiological hallmark of this early retinotopic visual ERP component (Clark et al., 1995; Jeffreys and Axford, 1972; Rauss et al., 2011, 2012). Following the C1, a P1m was recorded for the stimuli presented in the upper visual field, while a more lateralized P1 was recorded in response to stimuli presented in the lower visual field.

independent evidence for a genuine C1 response elicited for these peripheral visual distractors. As can be seen when comparing Figs. 4 and 6, the morphology, amplitude, latency and topography of the C1 component for the stimuli in the upper visual field are highly consistent across the main attention experiment and the localizer run. This confirms that joint effect of perceptual load and affective state during the main experiment unambiguously influenced this retinotopic visual evoked component generated in V1 early on following stimulus onset, during the sensory processing of these distractors.

Discussion

Our new ERP results show that the filtering of visual information exerted by attention control mechanisms in primary visual cortex is substantially influenced by the affective state of the participant. Increasing perceptual load at fixation produces a reduction of the perceptual encoding, taking place in V1, of a peripheral task-irrelevant distractor stimulus, in agreement with previous ERP and imaging results (Rauss et al., 2009; Schwartz et al., 2005), as well as attention selection models (Lavie, 2005; Rauss et al., 2011). However, this amplitude modulation of the C1 component with perceptual load was no longer evident when an increase in state anxiety or negative affect was transiently induced. Strikingly, even when the perceptual load was low, the amplitude of the C1 to the peripheral distractor was substantially reduced if the participant was in a negative affective state, suggesting that the concurrent internal state can rapidly influence attention selection processes following stimulus onset in V1. Furthermore, a set of control analyses establishes that these amplitude changes of the C1 component with load and affect concurrently were not accounted for by either component overlap or the rapid rise of a P1m component following the C1.

Negative affect narrows attentional focus

Previous studies stressed that attention selection is sharpened under anxiety or fear (Chajut and Algom, 2003; Finucane and Power, 2010; Wessel and Merckelbach, 1997). Moreover, previous results showed that negative affect can narrow the focus of attention, when measured either on a trial by trial basis (e.g., Fenske and Eastwood, 2003; Gable and Harmon-Jones, 2010), or using more tonic or sustained indices (Derryberry and Reed, 1998; Gasper and Clore, 2002). However, whereas these earlier studies had to rely on indirect behavioral correlates of attention selection processes (such as RTs during a flanker task, for example) to infer a link between emotion and attention, the strength of our approach is to provide a more direct cortical measure of sensory processing in V1 to neutral visual stimuli and its rapid influence by attention control brain processes. In this context, relatively "pure" effects of attention selection processes taking place in V1 can be compared across experimental conditions, ruling out possible confounds related to response selection processes or learned stimulus–response associations (see also Forster and Lavie, 2008).

Although effects of state anxiety, or less specifically, negative affect closely resemble effects of perceptual load during attention selection in V1, our results do not imply that an augmented aversive state simply mimics high load. Two observations allow us to rule out this account. First, task performance was strongly influenced by perceptual load, but not by emotion. Increasing load resulted in a decreased behavioral performance, but this effect was similar in the two affective conditions. Our supplementary analysis comparing the amplitude of the P300 before and after affect induction confirmed that the strong effect of load on this decision-related component (Kok, 2001) was stable in time and did not interact with transient changes in affective state. The lack of clear effects of state at the behavioral level during our attention task is not surprising, but in line with previous studies that failed to find impairments of task performance under stress or negative affect (Chajut and Algom, 2003; Hainaut and Bolmont, 2005; Moriya and Nittono, 2011; Moser et al., 2005; Shackman et al., 2011). Second, ERP results for the central target also clearly showed a genuine load-dependent modulation of the P300 component, but again this effect was not influenced by emotion, nor could it easily be accounted for by a dilution of this component across the three load levels. This former result is consistent with recent ERP findings (Moriya and Nittono, 2011) that failed to show any reliable modulation of the P300 despite the induction of negative mood through the exposure to unpleasant pictures. In our study, the use of negative cues challenging self-efficacy was clearly effective in modulating affective state and/or state anxiety levels (as confirmed by self-report measurements and changes in the spontaneous eye blink rate), but was probably not compelling enough to reliably deplete target-related ERP activities, such as reflected in changes of the P300 component (Schupp et al., 1997), unlike previously observed using other manipulations, such as direct exposure to fear-related stimuli (Moser et al., 2005) or threat of shock (Shackman et al., 2011). Future studies are needed to establish whether changes in state anxiety per se (such as typically achieved through threat exposure or fear induction), as opposed to changes in negative affect more generally (as likely found in our study), may differentially influence the processing (and corresponding VEPs) of central/task-relevant, compared to peripheral/task-irrelevant visual stimuli.

Negative affect influences the spatial encoding of the distractor

Previous ERP studies have clearly shown that the amplitude of the C1 is influenced not so much by the content of the stimulus, but rather by its spatial position in the visual field, consistent with an early retinotopic component generated along the calcarine fissure in the primary visual cortex (Clark et al., 1995). Moreover, previous results showed that attention allocation not only caused signal enhancement in the calcarine cortex (Desimone and Duncan, 1995; Hillyard et al., 1998), but also tuned receptive fields of neurons in V1, eventually leading to a sharpening of the spatial coding of attended visual stimuli (Fischer and Whitney, 2009). In light of these findings, our new ERP results for the C1 suggest that the primary feature or process that may be affected concurrently by load and affect is the actual perceptual encoding of the spatial position of the distractor stimulus shown in the upper visual field. In this framework, the effect of perceptual load in V1 would not necessarily correspond to a genuine gating effect (i.e. under high load, the sensory processing of the peripheral distractor would be reduced, relative to a low load condition), but alternatively, perceptual load (and negative emotional state) would somehow hamper the spatial encoding of the distractor in the periphery. Future studies are needed to disentangle these two possibilities and hence gain insight into the actual functional meaning of these early amplitudes changes found at the level of the C1 with perceptual load and affect concurrently.

Likely sources of affective sensory filtering in V1

Although our ERP results do not enable us to draw direct conclusions about the putative source of this compelling modulatory effect of the early neural response in V1, hints on the underlying neurophysiological mechanism can be formulated. Previous studies have pointed to a dorsal fronto-parietal network involved in the control of endogenous attention and exerting top-down influences in lower tier visual cortex, including V1 (Corbetta and Shulman, 2002; Fu et al., 2009; Lavie, 2005; Schwartz et al., 2005). Due to the similarities of the effects of attentional load and affective state on the C1 amplitude, we could assume that a similar mechanism is operating when either perceptual load is increased, or negative affect is transiently elicited. Alternatively, effects of state anxiety or more generally aversive states on early sensory processing in V1 might depend upon another non-overlapping neural mechanism, including changes in physiological arousal (Weiner and Concepcion, 1975). However, in our paradigm the concurrent recording of skin conductance during the task showed no significant difference between the mean SCL during the negative vs. positive affect condition, thus ruling out a simple interpretation in terms of changes in tonic arousal across these two affective conditions. Because our results also showed a sharp increase of the spontaneous eye blink rate following the presentation of negative (as opposed to positive) feedbacks, changes in early sensory processing in V1 may be interpreted as resulting from an enhanced stress response in this condition (Karson, 1983; Ponder and Kennedy, 1927). The spontaneous eye-blink rate has been linked indirectly to levels of dopamine activity as a state-dependent measure (Barbato et al., 2000; Taylor et al., 1999): the substantial increase in the blink rate following the presentation of negative performance feedbacks may thus reflect a phasic change in levels of dopamine, in particular in the frontal cortex (Abercrombie et al., 1989; Pani et al., 2000, for a review). Because excessive dopamine turnover in medial frontal structures can cause executive function impairments (Arnsten and Goldman-Rakic, 1998; Murphy et al., 1996), these dopaminergic-dependent neuromodulation effects triggered by the presentation of negative performance feedbacks (and as a result an increase in subjective levels of state anxiety) could potentially account for changes in early attentional filtering observed at the level of the C1 in our study during negative affective state.

Finally, the induction of anxiety or negative affect may also have been accompanied by the implementation of spontaneous emotion regulation strategies in these healthy adult participants (Gross, 2002 for a review; Kalisch et al., 2006), in such a way to overcome the experience of negative affect in this condition. This effect might partially deplete residual attention capacities that are not used for goal-directed behavior in the task (Bishop, 2007; Ochsner and Gross, 2005; Wager et al., 2008). This mechanism could potentially explain why under negative affect, the normal filtering of the distractor taking place in V1 is strongly enhanced. In this case, either medial prefrontal or cingulate regions would influence V1 processing rapidly following stimulus onset (Ochsner and Gross, 2005), or these modulatory effects taking place in V1 could depend on feedback projections from a more ventral brain system involved in the control of emotional attention (Sabatinelli et al., 2007; Vuilleumier, 2005). This mechanism could potentially explain why our affective manipulation does not influence goal-directed behavior, but mainly impairs the processing of “irrelevant” information (Chajut and Algom, 2003; Eysenck et al., 2007). Following these models, anxiety (or external stressors) primarily depletes attentional resources, and the capacity leftover is primarily allocated to the goal-relevant dimensions of the task at hand, while concurrent task-irrelevant information does not receive priority and is not deeply processed.

Two-stage model of attention selection influenced by affect

Besides a clear modulation of the C1 with load and affect, we found that immediately following this retinotopic component, the P1m deflection was also reliably influenced by these two factors, though showing a different pattern relative to the C1. Whereas amplitude variations of the P1 component as a function of attention selection have repeatedly been reported in the ERP literature (e.g., Hillyard and Anllo-Vento, 1998; Luck et al., 1990; Mangun and Hillyard, 1988; Martinez et al., 1999), only few studies have focused on this component when it is generated in response to desynchronized, task-unrelated stimuli presented at an unattended spatial location, as in the present case. While in one study (Handy et al., 2001, experiment 2), irrelevant probe stimuli elicited smaller P1 responses when the task at fixation was characterized by HL, another did not find variations of the P1 to irrelevant unattended stimuli when load was systematically changed (Barnhardt et al., 2008). By contrast, in our study, sharing similarities with the experiment of Barnhardt et al. (2008), we found an increase in P1m amplitude when the load level of the task at fixation increased. This finding suggests that, unlike the C1 modulations likely reflecting an early attentional gating process in V1, the apparent reduction of the P1 amplitude under LL potentially translates an active suppression mechanism operating in the extrastriate visual cortex (Luck et al., 1994), and aimed at downplaying the possible interference effect created by the distractor during early sensory stimulus processing. As such, these modulations of the P1m to the peripheral distractors with load would correspond to another, later attentional filtering mechanism relative to the C1 component, the former operating maximally during LL.

This interpretation is consistent with a two-stage attention process (see the hybrid load-theory of attentional selection, Lavie, 1995, 2005), whereby top-down filtering of irrelevant information already influences the amplitude of the C1 in the striate cortex if perceptual load is high, but a later attention effect takes place in the extrastriate visual cortex at the level of the P1m when the task does not exceed processing capacities, as during LL in the present study. In this model, increasing attentional load would mainly shift the temporal locus of the active filtering or suppression effect of irrelevant information within the visual cortex, from extrastriate (P1m) to striate cortex (C1 component). Notably, our new ERP results show that temporarily increasing affective state reliably influences this two-stage attention process taking place in the visual cortex early on following stimulus onset, indicated by a more efficient and earlier filtering of irrelevant information in this negative relative to a more positive affective state. This mechanism could eventually account for dynamic changes in attentional focus typically observed in several behavioral tasks after the induction of negative affect (Derryberry and Reed, 1998; Derryberry and Tucker, 1993; Easterbrook, 1959).

Conclusions

These new ERP results are consistent with the notion that the primary visual cortex is the locus of substantial interaction effects between attention and emotion control processes, early on following stimulus onset. Increasing perceptual load at fixation leads to a narrowing of processing capacities in V1, and as a result a reduction of the amplitude of the C1 component to unattended peripheral distractors. However our results show that this early bottleneck effect in V1 also depends on the internal state of the participant, since increases in levels of state anxiety or negative affect produce a concurrent load-like effect in V1 at the same early latency following stimulus onset. These effects therefore translate flexible filtering mechanisms taking place in V1 during early sensory processing.

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