

Positive emotion broadens attention focus through decreased position-specific spatial encoding in early visual cortex : evidence from ERPs

Naomi Vanlessen, Valentina Rossi, Rudi De Raedt, & Gilles Pourtois

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

Correspondence :

Gilles Pourtois

Department of Experimental-Clinical and Health Psychology

Ghent University

Henri Dunantlaan 2

9000 Gent, Belgium

Phone: +32 9 264 9144

Email: gilles.pourtois@ugent.be

Abstract

Recent evidence suggests that not only stimulus-specific attributes or top-down expectations can modulate attention selection processes, but also the actual mood state of the participant. In this study, we tested the prediction that the induction of positive mood can dynamically influence attention allocation and in turn modulate early stimulus sensory processing in primary visual cortex (V1). High-density visual event related potentials (ERPs) were recorded while participants performed a demanding task at fixation and were presented with peripheral irrelevant visual textures, whose position was systematically varied in the upper visual field (close, medium or far relative to fixation). Either a neutral or a positive mood was reliably induced and maintained throughout the experimental session. ERP results showed that the earliest retinotopic component following stimulus onset (C1) strongly varied in topography as a function of the position of the peripheral distractor, in agreement with a near-far spatial gradient. However, this effect was altered for participants in a positive, relative to neutral mood. On the contrary, positive mood did not modulate attention allocation for the central (task-relevant) stimuli, as reflected by the P300 component. We ran a control behavioral experiment confirming that positive emotion impaired attention allocation to the peripheral distractors, selectively. These results suggest a mood-dependent tuning of position specific encoding in V1 rapidly following stimulus onset. We discuss these new results against the dominant broaden-and-build theory.

Keywords: positive emotion, ERP, C1, attention, inhibition, selectivity, mood induction

INTRODUCTION

Sensory stimulus processing is not only determined by bottom-up physical characteristics, but also by top-down cognitive or affective processes. In this framework, mood has been shown to shape the way incoming information is attended and eventually processed (Gray, 2001, 2004). According to Fredrickson's influential broaden-and-build theory, negative and positive emotions have opposing but complementary functions (Fredrickson & Levenson, 1998): while negative emotions can narrow the thought-action repertoires of an individual, positive affect can substantially broaden thinking styles and these thought-action repertoires. Positive affective states elicit a broadening of the scope of attention (Derryberry & Reed, 1994), eventually enabling an open (Estrada, Isen, & Young, 1997), creative (Isen, Daubman, & Nowicki, 1987), integrative (Isen, Rosenzweig, & Young, 1991) and flexible (Isen & Daubman, 1984) way of thinking. In a similar vein, cognitive control abilities, and more specifically conflict adaptation, are reduced following the transient induction of positive mood (Van Steenbergen, Band, & Hommel, 2009, 2010).

Interestingly, recent findings suggest that a weakening of inhibitory control processes provides a plausible mechanism to account for a broadening of attention after the induction of positive emotion (Rowe, Hirsh, & Anderson, 2007; Wang et al., 2011). In this framework, loosening up inhibitory processes would result in a broader information processing style, and hence a less narrowed attention focus. As a result, individuals in a happy mood would become more receptive to irrelevant information, allowing distracting stimuli to interfere more strongly with goal-relevant stimuli (Dreisbach & Goschke, 2004). Thus, positive emotion would primarily reduce inhibitory control mechanisms (i.e., decrease attention selectivity), eventually leading to a less selective mode of stimulus processing, consistent with the predictions of the broaden-and-build theory. While this mechanism could, on the one hand, explain an enhanced distractibility under positive mood, it might, on the other hand, also

enable people to think in a more creative and flexible way, because they could learn more efficiently from incidental opportunities (Biss & Hasher, 2011; Biss, Hasher, & Thomas, 2010). Whereas many studies have already focused on these gains and drawbacks in higher level cognition and reasoning under positive mood (Ashby, Isen, & Turken, 1999; Biss & Hasher, 2011; Biss et al., 2010; Fredrickson, 2001; Fredrickson & Levenson, 1998; Isen, 2000), the actual *modus operandi* of positive emotion on attention abilities still remains largely underspecified. More specifically, an unanswered question is how positive emotion may dynamically shape and transform attention control mechanisms, such that a broader attentional scope can eventually bias early sensory stimulus processing, leading to the enhancement of both creativity and distractibility. A decreased attention control in this condition might underlie these behavioral phenomena.

Attention control usually refers to different brain mechanisms enabling a fast and efficient selection of relevant information in the environment (Desimone & Duncan, 1995; Posner, Snyder, & Davidson, 1980). Not only perceptual salience, novelty or unexpectedness determine the ease of attention selection (bottom-up factors; see Egeth & Yantis, 1997; Wolfe & Horowitz, 2004), but prior knowledge, expectations as well as mood reliably influence early sensory stimulus processing (top-down factors; see Corbetta & Shulman, 2002). Thus, both top-down and bottom-up attention processes exert control over sensory stimulus processing in such a way to gate the flow of incoming information, and eventually facilitate the selection of relevant stimuli, while filtering irrelevant information from further processing (Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Theeuwes, 2010). Interestingly, it has been suggested that prefrontal cognitive control regions are swiftly recruited in order to downplay the interfering effect potentially created by distractors, and eventually maintain an efficient attention selection process (Lavie, 2005; Lavie, Hirst, de Fockert, & Viding, 2004). However, these attention control systems are dynamic and not immune to changes in affective

states (see Desseilles et al., 2009; Gray, 2004; Rossi & Pourtois, 2012; Rowe et al., 2007). Nonetheless, effects of positive emotion on these attention control mechanisms eventually gating early sensory processing as early as in V1 have been much less explored than effects of negative emotion (Stolarova, Keil, & Moratti, 2006; West, Anderson, Ferber, & Pratt, 2011).

Accordingly, the goal of our study was to investigate, using state of the art Event Related Potentials (ERP) methods (Experiment 1) and standard behavioral measures (Experiment 2), possible downside effects of positive mood on early sensory stimulus processing, presumably resulting from a change in top-down attention control mechanisms. Participants performed a demanding task at fixation, while distractors were presented in the upper visual field at an unpredictable time and location relative to these task relevant stimuli (Schwartz et al., 2005). This set up is suited to explore, using high density EEG measurements, changes in the spatial gradient of visual attention towards the peripheral distractors, while fixation is maintained at a constant location in the center of the screen (Pourtois, Delplanque, Michel, & Vuilleumier, 2008; Rauss, Schwartz, & Pourtois, 2011; Rossi & Pourtois, 2012). Because we used eccentric/peripheral visual stimuli, we could record a reliable C1 ERP component reflecting an early retinotopic encoding of the stimulus in V1, being however sensitive to top-down attention control effects (Rauss, Pourtois, Vuilleumier, & Schwartz, 2009; Rauss et al., 2011; Rossi & Pourtois, 2012). The C1 usually peaks ~50-100 ms after stimulus onset over central occipito-parietal scalp positions (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Jeffreys & Axford, 1972). In accordance with the cruciform organization of the primary visual cortex and calcarine fissure, the amplitude and polarity of the C1 substantially change as a function of the position of the stimulus in the visual field (Clark, Fan, & Hillyard, 1995).

In Experiment 1, we therefore capitalized on these well-defined electrophysiological properties and investigated whether the C1 component could vary in size and topography not

only according to the actual position of the distractor stimulus shown in the upper visual field (i.e. larger negative component for position close to fixation, relative to far), but also with the actual mood of the participant (either happy or neutral). We tested the prediction that the selectivity for early spatial encoding of distractors in V1, at the level of the C1, would decrease after the induction of positive mood. This effect could result from a modulation of top-down attention control mechanisms by positive mood (Rowe et al., 2007), eventually resulting in a decreased position specific selectivity at a more basic perceptual level. More precisely, we surmised that the normal reduction of the C1 with increasing distance of the distractor, relative to fixation, would be less pronounced in participants in a positive mood, relative to a neutral mood, consistent with broadening of attention.

We also explored possible effects of positive mood on later ERP components in response to the peripheral distractors. Unlike the striate C1, the extrastriate P1, peaking ~100-150 ms post stimulus onset over occipital leads, is mostly sensitive to the content and not to the position of the stimulus within the visual field (Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Herrmann & Knight, 2000; Martinez et al., 1999), but can also vary depending on the affective state of the participant (Moriya & Nittono, 2011). Moreover, the amplitude of the P1 is typically larger for attended, relative to unattended stimuli, consistent with a gain control mechanism of visual attention exerting modulatory effects in the extrastriate visual cortex (Hillyard & Anllo-Vento, 1998; Martinez et al., 1999). Finally, we were also interested in possible effects of mood on the processing of central, task relevant stimuli. The efficiency of central target stimulus processing was mostly assessed by means of the decision-related P300 component, whose amplitude strongly varies with the amount of resources allocated to task demands (Ericsson, Olofsson, Nordin, Rudolfsson, & Sandstrom, 2008; Kok, 2001; Polich, 2007; Polich & Kok, 1995). Moreover, because this component was recently shown to vary with the (negative) affective state of the participant (e.g., Shackman,

Maxwell, McMenamin, Greischar, & Davidson, 2011), we tested whether attention allocation towards central (task-relevant) stimuli could also be altered after the induction of positive mood or not.

To corroborate the assumption of a drop in early attention selectivity for the peripheral textures following the induction of positive mood, we ran an additional behavioral experiment. In Experiment 2, participants were asked to explicitly discriminate the content of these peripheral stimuli (in addition to the centrally-presented stimuli at fixation). We reasoned that if the effect of positive mood may correspond to a change in prefrontal attention control mechanisms, and hence early sensory stimulus selectivity, the visual processing of these peripheral stimuli may be impaired, compared to a control condition (i.e. neutral mood).

Previous research has shown that an increased attentional scope is associated with a loss in spatial resolution and processing efficiency, as compared to a detailed processing when the attentional scope is narrowed around a specific portion of the visual field (Carrasco, 2011; Castiello & Umiltà, 1990, 1992; Eriksen & Yeh, 1985; Ivry & Robertson, 1998; Muller, Bartelt, Donner, Villringer, & Brandt, 2003). Thus, if positive mood can broaden the attentional scope, processing over larger portions of the space can cause a drop in spatial resolution, compared to a smaller attentional scope in a neutral mood. Hence, such an impairment in early spatial encoding selectivity would in turn constrain the capacity to perform a visual discrimination of the peripheral stimuli based on the processing of local (geometric) features.

Experiment 2 also enabled us to confirm whether the processing of the centrally-presented stimuli would be unchanged in a positive mood, relative to a neutral mood, in line with the results obtained in Experiment 1.

METHODS

Participants

We tested 70 participants who were all right-handed, had normal or corrected-to-normal vision and no history of psychiatric or neurologic disorder according to a self-report questionnaire. All participants were undergraduate psychology students from Ghent University and all gave written informed consent prior to participation. From the thirty-four participants recruited for Experiment 1 (age: $M = 22$; $SD = 2$; 7 males), seventeen were randomly assigned to the positive mood condition and seventeen to the neutral mood condition. One participant in the neutral mood group reported not being able to use imagery, making the implementation of the mood induction procedure (MIP) impossible. Therefore, data for this participant were excluded from further analyses. In Experiment 2, 36 undergraduate students (age: $M = 19$; $SD = 1$; 3 males) were randomly assigned either to the neutral or positive mood condition (18 participants per condition). The data of one participant from the neutral mood group were excluded from further analysis because of excessive slow RTs for the detection of central targets (mean ± 2.5 SDs). Results are reported for the 35 remaining participants. Subjects participated in exchange for course credits (32) or financial compensation (38).

Materials

Mood Induction. We used a between-subjects design to induce either a sustained positive or a neutral/control mood, suited to avoid possible carry-over effects between different mood conditions. Participants were naïve regarding the purpose of the MIP. A cover story was told in order to make participants believe that the experiment concerned the relationship between the processing of visual information and the use of imagination. Mood was induced by means of an imagery procedure where participants were instructed to vividly imagine reliving a happy or neutral autobiographical memory (Holmes, 2006; Holmes, Coughtrey, & Connor, 2008). First, participants were trained in taking a field perspective (i.e. imagining from one's

own perspective) during mental imagery (Holmes, 2006; Holmes et al., 2008). Next, participants were instructed to recall and report an event that happened on a specific day, more than one week ago, which made them feel either very happy (positive mood group) or that did not elicit any specific emotion (neutral mood group) using episodic memory. Participants were then asked to close their eyes and to vividly imagine reliving the recalled experience. Participants were encouraged to use concrete visualizations and to take the requested field perspective while imagining (Watkins & Moberly, 2009; based on Holmes et al., 2008). Participants then imagined the recalled experience for 30 seconds (twice), interrupted by questions about what they could see, hear and feel (based on Watkins & Moberly, 2009). Classical music fragments started to play during the memory recall and continued to play throughout the experiment sessions, such that the music would serve as implicit trigger for the corresponding mood. In Experiment 1, the same (neutral) music samples were played in both mood groups in order to balance possible interference effects created by the music on the recorded EEG signal. However, in order to elicit stronger mood inducing effects and a conditioned context that was better adjusted to the targeted mood, we used ‘happy’ music in the positive mood condition and neutral music in the neutral mood condition in Experiment 2¹. These music samples were validated in previous research (Bower & Mayer, 1989; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007).

To measure subjective levels of mood, participants were asked to indicate how they felt using the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988) and three 10 centimeters, horizontal Visual Analogue Scales (VAS) for feelings of

¹We performed a control study (n=15) to assess if the music samples alone, without the MIP, could have influenced the behavioral results in Experiment 2. Therefore, participants performed the dual attention task while either positive music fragments (3 blocks) or neutral music fragments (3 other blocks) were played in the background. Subjects were instructed to pay no specific attention to the music. No MIP was administered. The results showed that neutral and positive music samples did not differentially influence accuracy or RTs for the central task, nor for the discrimination of peripheral textures, suggesting that the MIP, and not the use of different music samples alone, modulated attention allocation in the upper visual field (Experiment 2).

happiness, pleasantness and sadness. The left anchor of the VAS was labeled ‘Neutral’, while the right one was labeled ‘As happy/pleasant/sad as you can imagine’.

Attention Task. We adapted a standard experimental paradigm (Schwartz et al., 2005; Rauss et al., 2009; Rossi & Pourtois, 2012). The task was programmed using E-Prime, Version 2 (Psychology Software Tools, Inc., 2001). Participants were instructed to carefully attend to a rapid serial visual presentation (RSVP) of short tilted lines (1 cm) at central fixation (Figure 1). In Experiment 1, participants silently counted the occurrences of deviant lines within each block and reported this value at the end of the block, while in Experiment 2 they were instructed to press a key with their left finger whenever they could detect online the occurrence of a deviant line. Deviant lines were tilted 45° and standard lines 35° counterclockwise from the vertical axis. The ratio standard/target was 4:1, with the number of deviant lines varying between 8 and 12 per block. Because previous studies have confirmed that this task requires central/foveal vision and sustained attention (see Rauss et al., 2009; Rossi & Pourtois, 2012; Schwartz et al., 2005), we used it to ascertain that participants were fixating at the center of the screen where these short lines were presented. Decoupled from this central RSVP, uniform visual textures were shown in the upper visual field at an unpredictable location (i.e. one out of three locations) and time (i.e. variable SOA between central stimulus offset and peripheral texture onset) relative to the central stimuli (Figure 1AB). The experiment consisted of a total of 300 central stimuli (i.e., 240 standard and 60 target lines), and 150 peripheral stimuli (i.e., 120 after the presentation of a central standard line and 30 after a central target line). The peripheral stimuli consisted of two arrays of quadrangle elements forming a homogenous visual texture ($3^\circ \times 34^\circ$ of visual angle), briefly flashed in the upper visual field at 5.3° (Close), 7.8° (Medium) or 10.3° (Far) from central fixation (see Figure 1A). Two different types of quadrangle elements (0,5 cm wide x 0,4 cm high or 0,6 cm wide x 0,3 cm high, see Figure 1C) were used, with 25 presentations of each

type at each location. These peripheral textures were task-irrelevant (i.e., distractors) in Experiment 1, as opposed to Experiment 2 where participants were invited to discriminate the actual content of visual textures (either type 1 or 2, based on the actual quadrangle elements; i.e., dual task setting). In the latter experiment, a fixation cross was presented again at the offset of the visual texture and remained on the screen until participants pressed one out of two keys using their right hand (stimulus-response mapping was alternated across participants). A reminder of the stimulus-response mapping was shown at the beginning of each block. Stimuli were gray and presented against a uniform black background. Participants were seated at 57 cm in front of a 19" CRT screen, with their head movements restrained by a chinrest.

Localizer. In order to identify the C1 and obtain independent evidence that the earliest visual ERP component recorded during the main attention task for the peripheral textures genuinely corresponded to a retinotopic C1, we administered to participants of Experiment 1 two extra blocks of peripheral textures only, under passive viewing conditions at the end of the experimental session (see Rossi & Pourtois, 2012). In these blocks, no RSVP was imposed at fixation. In each block, 120 stimuli were presented in random order, with an even number of presentations at six possible locations (upper or lower visual field: close, medium, or far from fixation). The localizer blocks were administered at the end of the experiment in order to avoid unwanted priming effects, since they remained fully task-irrelevant in Experiment 1, in agreement with previous research (e.g. Rossi & Pourtois, 2012). Moreover, residual effects of (positive) mood were expected to be minimal during these final blocks, because no repetition of the MIP took place prior to them.

Procedure

In Experiment 1, participants were first prepared for EEG recording. Participants completed a practice session containing two blocks of 20 trials (in total, 32 standard lines, 8 target lines),

which were repeated until 80% of the (deviant) central lines were reported correctly. Next, positive or neutral mood was induced by means of the MIP, which was shortly (5 min) repeated at the end of Block 3 in order to maintain the targeted mood throughout the experimental session. Participants completed six different blocks of 50 trials each of the attention task. Each trial started with the presentation of a fixation cross (250 ms), followed by a central line (150 ms) at the same location (see Figure 1B) and again a fixation cross, displayed for the duration of the SOA (average duration in Experiment 1: 375 ms, randomly varying between 250 and 500 ms; in Experiment 2: 625 ms, randomly varying between 500 and 750 ms). After the SOA, in half of the trials a visual texture was flashed for 250 ms at one of three possible locations in the upper visual field; in the other half of the trials, only the fixation cross remained on screen for the same interval. Trials were presented in a semi-random order. The first three stimuli in a block never contained a target line, nor a peripheral distractor. Instructions emphasized the highest accuracy possible for the task at fixation (Experiments 1-2), as well as both accuracy and speed for the two-alternative forced choice task performed with the peripheral textures (Experiment 2). In addition, instructions given to participants of Experiment 2 clearly emphasized the importance of a high accuracy for the primary task at fixation and the need to maintain attention focused at this central location throughout the whole experiment. VASs and PANAS were administered at the beginning of the experiment (baseline measure), after each MIP, and at the end of the experiment in order to observe possible changes in mood before, during and after the MIP.

Once the experimental session was completed, participants filled out four trait-related/personality questionnaires: the Beck Depression Inventory (BDI; Beck, Steer, Ball, & Ranieri, 1996), the Spielberger State-Trait Inventory – trait version (STAI-T; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983), the BIS/BAS scales (Carver & White, 1994) and the Spontaneous Use of Imagery Scale (Reisberg, Pearson, & Kosslyn, 2003).

To sum up, in both Experiment 1 and 2, participants performed a main oddball detection task at fixation, whereas peripheral textures were briefly flashed during the ISI in the upper visual field at an unpredictable time and location. However, in Experiment 2, these peripheral textures were task-relevant and they required an overt visual discrimination, while in Experiment 1 (EEG) they remained task-irrelevant. Additional methodological differences between the two experiments concerned (i) the music played in the background during the experiment (i.e. same neutral samples for both groups in Experiment 1 vs. neutral or positive samples in Experiment 2), and (ii) specific task demands for the central stimuli (i.e. in Experiment 1, the deviant lines had to be detected and counted silently by the participants before reporting this number at the end of each block, whereas in Experiment 2, participants had to make online a specific key press whenever detecting them).

Analyses of behavioral data

Changes in mood were verified by comparing post to pre-MIP subjective measures of affect. We first computed post-MIP average scores for each VAS and the PANAS administered after the two MIPs and at the end of the experiment. Next, we performed a 2 (Time: baseline vs. post-MIP) x 2 (Mood: neutral vs. positive) mixed ANOVA on the VASs and the PANAS scores, followed by independent T-tests (planned comparisons). For the four trait-related questionnaires, mean scores were calculated and compared between groups in order to check for possible uncontrolled personality differences between groups.

In Experiment 1, accuracy for the oddball task at fixation was computed for each participant separately by subtracting the reported number from the actual number of deviant lines and the sum of these deviations was computed for the six blocks. Next, these numbers were compared between groups using an independent Student T-test. In Experiment 2, accuracy and reaction times (RTs) for the central task were compared between groups using independent t-tests. Performance for the peripheral textures (accuracy and RTs) was analyzed

using mixed ANOVAs, with the within-subject factor Distance (close, medium or far) and the between-subject factor Mood (positive vs. neutral). Trials with errors on the central task, as well as RTs exceeding ± 2.5 SDs above or below the individual mean RT on both central and peripheral tasks were excluded from further analysis. The exclusion rate did not differ between the two mood groups (positive: $M = 9.57\%$, $SD = 3.70$; neutral: $M = 7.94\%$, $SD = 3.48$), $t(33) = 1.34$, $p = 0.19$). Statistical analyses were run on 91.22% of the total data.

Greenhouse-Geisser correction was applied when assumptions of sphericity were violated. In these cases, we reported corrected p-values and uncorrected degrees of freedom.

EEG data acquisition and reduction

EEG data were recorded from 128 electrodes placed according to the extended 10-20 EEG system using an elastic cap (Biosemi Active Two System). Vertical and horizontal eye movements were recorded by means of additional bipolar electrodes placed respectively above and below the left eye, and on the outer canthi of both eyes. EEG signals were referenced online to the CMS-DRL ground and continuously sampled at 512 Hz.

EEG signals were referenced offline to the linked mastoids, using Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany). Band-pass filters between 0.016 and 70Hz and a notch-filter (50Hz) were used. The filtered data were then segmented into stimulus-locked epochs using a segmentation window of 100 ms pre- and 800 ms post-stimulus onset. Eye-blink artifacts were automatically corrected by means of the standard procedure put forward by Gratton and colleagues (Gratton, Coles, & Donchin, 1983), and individual epochs were baseline corrected using the entire pre-stimulus interval. Epochs of the EEG containing residual artifacts exceeding $\pm 75\mu V$ were semi-automatically rejected. Noisy electrodes were interpolated using a spherical splines procedure. Individual averages were computed, separately for each condition. Finally, a 30Hz low-pass filter was applied before the calculation of grand average waveforms.

To characterize and analyze ERPs to the peripheral distractors, we performed a detailed ERP topographic mapping analysis. The added value and underlying principles of this data-driven analysis have been described extensively elsewhere (Michel, Seeck, & Landis, 1999; Murray, Brunet, & Michel, 2008; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Pourtois, De Pretto, Hauert, & Vuilleumier, 2006; Pourtois et al., 2008; Pourtois, Thut, de Peralta, Michel, & Vuilleumier, 2005). Since the C1 is primarily a location-sensitive early visual ERP, the exact same stimulus elicits a different topography and strength of the C1 electric field depending on its actual position in the peripheral visual field (Clark et al., 1995). Accordingly, we used a standard ERP topographic mapping analysis able to capture these changes in the expression of the electric field (i.e. topography) of the C1 as a function of stimulus position. Using a K-means spatial cluster analysis, we first identified in the grand average data the dominant scalp topographies corresponding to the C1 (95-115ms post-stimulus onset) and P1 (165-185ms post-stimulus onset) components generated in response to the peripheral distractors, as well as P300 (400-600 ms post-stimulus onset) in response to the centrally-presented line stimuli. The following standard parameters were used: average reference; number of random trials: 100; smoothing strength (Besag factor) of 10; smoothing half window size of 3; merging of clusters correlating above 0.92; rejection of segments less or equal to 3 time-frames; no sequentializing. These topographic maps were determined objectively using both cross validation (Pascual-Marqui, Michel, & Lehmann, 1995) and Krzanowski-Lai criteria (Pascual-Marqui et al., 1995; Tibshirani, Walther, & Hastie, 2001). Following standard practice, these dominant scalp topographies were then fitted back to the ERPs of each individual participant using spatial fitting procedures to quantitatively determine their representation across subjects and conditions. The Global Explained Variance (GEV, or goodness of fit) was then used as main dependent variable in standard parametric statistical analyses of variance (ANOVAs) to verify, on the one hand

whether mood and position reliably influenced the C1 and/or P1 in response to the peripheral textures, and on the other hand, if mood and stimulus type (standard or target) modulated the P300 in response to task-relevant stimuli.

RESULTS

Experiment 1

Changes in mood: manipulation check

The 2 (Time) x 2 (Mood) mixed ANOVA on the VAS scores showed a significant interaction effect between Time and Mood for feelings of happiness (baseline: positive: $M = 4.48$, $SD = 2.83$, neutral: $M = 4.80$, $SD = 2.92$; post-MIP: positive: $M = 7.57$, $SD = 1.16$, neutral: $M = 4.32$, $SD = 3.00$, $F(1,31) = 23.83$, $p < 0.001$), and pleasantness (baseline: positive: $M = 4.89$, $SD = 2.72$, neutral: $M = 4.30$, $SD = 3.13$; post-MIP: positive: $M = 7.57$, $SD = 1.12$, neutral: $M = 4.66$, $SD = 3.00$, $F(1,31) = 10.21$, $p = 0.003$). Next, we compared VAS scores between the positive and the neutral mood group at baseline vs. post-MIP, separately. Independent T-tests showed, as expected, no difference for reported happiness ($t(31) = 0.32$, $p = 0.75$), nor pleasantness ($t(31) = 0.43$, $p = 0.56$) between mood groups at baseline. However, post-MIP mood measurements showed a significant difference between the positive and the neutral mood group for feelings of happiness ($t(31) = 4.14$, $p < 0.001$), and pleasantness ($t(31) = 3.78$, $p = 0.001$; see Figure 2). The 2 (Time) x 2 (Mood) mixed ANOVA for the sadness VAS did not show a significant interaction effect (baseline: positive: $M = 0.73$, $SD = 0.97$, neutral: $M = 0.44$, $SD = 0.54$; post-MIP: positive: $M = 0.51$, $SD = 0.73$, neutral: $M = 0.34$, $SD = 0.40$, $F(1,31) = 0.44$, $p = 0.51$). These results confirmed a significant and selective increase in positive affect after MIP in the positive mood group, but no such change in the neutral mood group.

The 2 (Time) x 2 (Mood) mixed ANOVA on the PANAS scores showed a significant interaction effect between Time and Mood group for the PA scales (baseline: positive: $M = 32.65$, $SD = 5.53$, neutral: $M = 32.88$, $SD = 5.26$; post-MIP: positive: $M = 34.96$, $SD = 4.63$, neutral: $M = 30.54$, $SD = 7.28$, $F(1,31) = 8.69$, $p = 0.006$), but not for the NA scales (baseline: $M = 23.56$, $SD = 5.81$; post-MIP: $M = 10.89$, $SD = 1.86$, $F(1,31) = 1.24$, $p = 0.27$). An independent T-test (PA scales) showed a significant difference between positive and neutral mood group post-MIP, $t(31) = 2.09$, $p = 0.04$. At baseline, this difference was not significant ($t(31) = 0.54$, $p = 0.90$).

Behavioral results.

On average, participants in both mood groups had low error rates (sum of absolute deviations in positive group: $M = 4.29$, $SD = 2.78$; neutral group: $M = 4.88$, $SD = 5.60$). There was no significant group difference in accuracy ($t(31) = 0.38$, $p = 0.71$; see Figure 3B), suggesting that behavioral performance for the central task was high and balanced between the two mood groups.

ERP results.

P300. The topographical mapping analysis identified three main clusters/topographies during the P300 time interval following the onset of the central tilted lines. We compared the mean GEV values obtained for these three dominant maps using a mixed ANOVA with Stimulus type (standard vs. target) and Map configurations ($n=3$) as within subjects factors, and Mood (positive vs. neutral) as a between subjects factor. The results showed a significant effect of Stimulus type ($F(1,31) = 4.385$, $p < 0.05$), and a significant interaction effect between Stimulus type and Map configuration ($F(2,62) = 15.180$, $p < 0.001$) showing that the configuration of the P300 substantially changed depending on the stimulus type (see Figure4), in line with previous research (Kim, Kim, Yoon, & Jung, 2008; Kok, 2001; McCarthy & Donchin, 1981; Sawaki & Katayama, 2007). Importantly, no significant main effect of Mood

was found ($F(1,31) = 0.016, p = 0.90$), nor a significant interaction effect between Mood and Map configuration ($F(2,62) = 0.035, p = 0.96$), indicating that participants in both groups processed standard vs. target central stimuli differentially.

C1. Two main topographies were found during the C1 time window (95-115ms; see Figure 5A) following the onset of the peripheral textures. A mixed ANOVA with Map configurations ($n=2$) and Distance (close, medium or far) as within subjects factors, and Mood (positive vs. neutral) as between subject factor was performed on the GEV values extracted for these two C1 topographies. The results showed a significant main effect of Distance ($F(2,62) = 7.737, p = 0.001$), and a significant interaction effect between Distance and Mood ($F(2,62) = 8.035, p = 0.001$). Whereas the former effect confirmed that the topography of the C1 component reliably changed depending on the position of the stimulus in the upper visual field, the latter interaction effect suggested that the induced positive mood influenced this position-specific encoding of the distractor (as reflected by the C1 topography). Planned comparisons revealed a significant drop of the GEV of the dominant C1 map (i.e. being maximum for the position close relative to fixation) as a function of distance in the neutral mood group (Close vs. Medium, $t(15) = 2.71, p = 0.02$; Close vs. Far, $t(15) = 2.50, p = 0.03$), consistent with a non-linear spatial gradient effect. However, this effect was not observed for the C1 of participants in the positive mood group (Close vs. Medium, $t(16) = 0.39, p = 0.70$; Close vs. Far, $t(16) = 1.20, p = 0.25$; see Figure 5BC). In this group, the explained variance of the dominant C1 topography was not significantly different across the three spatial positions, suggesting a broadening of attention. Together, these results suggest a link between changes in positive mood and position-dependent early brain responses in V1 to these (unattended) textures shown in the upper visual field.

Three dominant maps were found during the C1 time window (95-115ms) for the ERP data recorded during the localizer (upper visual field, see Figure 6), whereas two dominant C1

maps were found for the C1 recorded during the main task. Presumably, this discrepancy may tentatively be explained by the different task demands (and stimulus parameters for the central stimuli) between these two sessions. Because peripheral textures used in the localizer and in the main task were identical but embedded in different experimental contexts, it is likely that the topographical segmentation data analysis identified slight differences in the actual expression of the C1 map across these two sessions.

A mixed ANOVA with Map configurations ($n=3$) and Distance (close, medium or far) as within subjects factors and the between subjects factor Mood (positive vs. neutral) was performed on the GEV values extracted for these maps (localizer). The ANOVA showed a significant interaction effect between Distance and Map ($F(2, 62) = 7.71, p < 0.001$), while the Mood and Map ($F(2,62) = 0.758, p = 0.47$) as well as Mood and Distance ($F(2,62) = 1.53, p = 0.22$) interactions were non-significant, suggesting a similar early retinotopic encoding of the peripheral textures in both groups. These results suggest that, unlike the C1 recorded during the main attention task, the C1 elicited by the same peripheral distractors during the localizer run (passive viewing) was not reliably influenced by mood. Importantly, a systematic comparison of topographies and waveforms for the C1 deflection recorded during the localizer vs. main attention task to the same peripheral textures confirmed that this early negative component unambiguously corresponded to a genuine C1 deflection, showing the expected polarity reversal as a function of the lower vs. upper visual presentation (see Figure 6).

P1. During the time interval of the P1 (165-185ms) following the onset of the peripheral textures (main task), a single dominant topographical component was found to account for the ERP signal across the three positions (close, middle or far; see Figure 5A). A mixed ANOVA with Distance (close, medium, far) as within subjects factor and Mood (positive, neutral) as between subject factor on the GEV values extracted for this dominant P1 topography did not

show any systematic variation with the position of peripheral textures ($F(2,62) = 2.06, p = 0.14$), confirming that this extrastriate component was most likely responding to the content, rather than the position of these stimuli. Moreover, this analysis showed that there was no significant main effect of Mood ($F(1,31) = 1.11, p = 0.30$), nor a significant interaction effect between Mood and Distance ($F(2,62) = 0.85, p = 0.43$).

Questionnaires

T-tests performed on the questionnaire data failed to reveal any significant group difference (BDI: $t(31) = 0.29, p = 0.78$; STAI-T: $t(31) = 0.30, p = 0.77$; SUIIS: $t(31) = 0.08, p = 0.23$, BIS/BAS, BIS: $t(31) = 0.53, p = 0.60$, BAS Drive $t(31) = 0.61, p = 0.55$, BAS Fun: $t(31) = 0.12, p = 0.91$, BAS Reward: $t(31) = 0.09, p = 0.93$), suggesting that the observed ERP differences for the processing of the peripheral textures between the two groups could not be explained by uncontrolled group differences along these specific personality traits.

Experiment 2

Changes in mood: manipulation check

The 2 (Time) x 2 (Mood) mixed ANOVA on the VAS scores showed a significant interaction effect between these two factors for feelings of happiness (baseline: positive: $M = 7.11, SD = 1.29$, neutral: $M = 7.28, SD = 0.87$; post-MIP: positive: $M = 8.37, SD = 1.04$, neutral: $M = 7.46, SD = 1.12, F(1,33) = 15.07, p < 0.001$) and pleasantness (baseline: positive: $M = 7.08, SD = 1.25$, neutral: $M = 7.32, SD = 0.83$; post-MIP: positive: $M = 8.16, SD = 1.06$, neutral: $M = 7.69, SD = 1.10, F(1,33) = 4.51, p = 0.04$; see Figure 2), but not for feelings of sadness (baseline: positive: $M = 1.33, SD = 1.56$, neutral: $M = 0.75, SD = 0.66$; post-MIP: positive: $M = 0.61, SD = 0.55$, neutral: $M = 0.58, SD = 0.41, F(1,33) = 2.41, p = 0.13$). Planned comparisons confirmed that there was no significant group difference at baseline in reported feelings of happiness ($t(33) = 0.450, p = 0.51$), pleasantness ($t(33) = 0.665, p = 0.656$), nor sadness ($t(33) = 1.409, p = 0.17$). Post-MIP VAS scores differed significantly between

positive and neutral mood group for feelings of happiness ($t(33) = 2.481, p = 0.018$), but did not reach significance for pleasantness ($t(33) = 1.306, p = 0.20$) or sadness ($t(33) = 0.215, p = 0.83$). Altogether, these results confirmed an increase in happiness after the MIP in the positive mood group, but no change in the neutral mood group.

By contrast, the 2 (Time) x 2 (Mood) mixed ANOVA on the PANAS scores showed no significant interaction effect for the PA scales (baseline: $M = 32.40, SD = 5.41$; post-MIP: $M = 32.19, SD = 5.44, F(1,33) = 1.97, p = 0.17$), nor for the NA scales (baseline: $M = 12.34, SD = 2.33$; post-MIP: $M = 11.26, SD = 1.56, F(1,33) = 0.28, p = 0.60$).

Attention task

Central stimuli. Participants' accuracy was high in both groups (positive: 88.65%, $SD = 6.66$; neutral: 91.84%, $SD = 6.05$). There was no significant difference between the two groups in accuracy ($t(33) = 1.49, p = 0.15$; see Figure 3B). Neither the amount of false alarms, (positive: $M = 4.89, SD = 9.06$; neutral: $M = 2.41, SD = 3.62, t(33) = 1.05, p = 0.30$), nor omissions (positive: $M = 22.17, SD = 10.83$, neutral: $M = 17.71, SD = 10.39, t(33) = 1.24, p = 0.22$), differed significantly between the two groups. Likewise, RTs for correct detections were balanced between groups (positive: $M = 499.70, SD = 97.68$; neutral: $M = 456.22, SD = 61.66, t(33) = 1.56, p = 0.13$).

These results confirmed that participants correctly attended and maintained fixation to the central RSVP, and that positive mood induction did not simply affect the processing of these centrally-presented lines, relative to neutral mood.

Peripheral stimuli. The 2(Mood: neutral vs. positive) x 3(Distance: close, medium, or far) mixed ANOVA performed on the mean accuracy scores revealed a significant main effect of distance ($F(2,66) = 16.10, p < 0.001$), showing, as expected, a monotonic decrease of performance as a function of distance relative to fixation (Figure 3A): position close, $M = 80.14, SD = 15.62$; position medium, $M = 78.03, SD = 15.14$; position far, $M = 69.96, SD =$

14.33. Accuracy differed significantly between positions far and medium ($t(33)= 4.13, p < 0.001$), as well as between far and close ($t(33)= 4.83, p < 0.001$). However, mean accuracy did not differ significantly between close and medium ($t(33)= 1.41, p = 0.17$). Importantly, this analysis also revealed a significant main effect of mood, indicated by an overall lower accuracy in the positive mood group ($M = 71.22, SD = 12.57$) when compared to the neutral mood group ($M = 80.15, SD = 13.11, F(1,33) = 2.23, p = 0.03$; see Figure 3A). The interaction effect between Mood and Distance was not significant ($F(2,66) = 0.36, p = 0.70$), indicating that the effect of mood did not differ across the three positions. Planned comparisons showed a significant difference between positive and neutral mood group for position far ($t(33)= 2.43, p = 0.02$) and for position close ($t(33)=2.13, p = 0.04$), but no such difference between positive and neutral mood group for position medium ($t(33)= 1.61, p = 0.12$). Hence, accuracy with the peripheral textures was overall lower for participants in a positive mood, relative to a neutral mood. This result may be interpreted as a general drop in attention selectivity for the textures shown in the upper visual field for participants with a positive mood².

Analysis of RTs for correct responses confirmed that distance reliably influenced the speed in a predictive way ($F(2,66) = 13.49, p < 0.001$), with faster decisions for peripheral textures shown close to fixation ($M = 517.73, SD = 136.01$), relative to the medium position ($M = 564.06, SD = 155.62, t(34) = 3.72, p < 0.001$), or far position ($M = 582.87, SD = 151.21, t(34)= 4.49, p < 0.001$). The RT difference between medium and far was not significant ($t(33)= 1.44, p = 0.16$). There was a significant interaction effect between Mood and Distance ($F(2,66) = 3.13, p = 0.05$), showing a monotonic increase of RT with increasing distance from

²When we analyzed the changes in levels of positive mood following the MIP (taking into account VAS and PANAS scores concurrently), we found that 7 out of 35 participants showed an unusual pattern. Three participants assigned to the neutral mood group showed an increase in positive mood while four participants assigned to the positive mood group showed a weak or no increase in positive mood following the MIP. We performed additional refined statistical analyses excluding the data of these 7 subjects but we did not observe any change in the performance for the central task (effect of group was still non-significant; $t(26) = 1.18, p = 0.25$), nor for the visual discrimination of the peripheral textures (effect of group was still significant; $F(1,26) = 4.50, p < 0.05$).

fixation in the neutral mood group, but not for the positive mood group. No main effect of Mood was found ($F(1,36) = 1.04, p = 0.32$).

Questionnaires

Comparisons performed on the personality questionnaire data failed to reveal any significant difference between the two mood groups (BDI: $t(33) = 0.25, p = 0.80$; STAI-T: $t(33) = 0.39, p = 0.70$; SUIIS: $t(33) = 0.25, p = 0.80$; BIS/BAS: BIS: $t(33) = 0.26, p = 0.80$, BAS Drive: $t(33) = 0.31, p = 0.76$, BAS Reward Responsiveness: $t(33) = 0.82, p = 0.42$ scales), except for the BAS Fun Seeking scale, with a (marginally) significantly higher score in the neutral ($M = 6.59, p = 1.12$) compared to the positive ($M = 5.44, p = 2.09$) mood group ($t(33) = 2.00, p = 0.054$).

DISCUSSION

The results of our study show that positive mood can alter the earliest cortical stage of stimulus processing, presumably taking place in V1 (i.e. C1 component; Rauss et al., 2011). More specifically, our ERP findings show that the expression (topography) of the C1 to unattended peripheral distractors shown in the upper visual field strongly varies according to the position (close, medium or far) of these textures relative to central fixation. However, this early spatial gradient effect is clearly altered during positive, relative to neutral, mood. In line with a broadening of spatial attention with positive emotion, the dominant topography of the C1 was equally strong regardless of the position of the texture in the upper visual field for participants experiencing positive affect, whereas the C1 of participants in the neutral mood condition showed a clear and sharp topographical change according to the same manipulation (see Figure 5BC). Importantly, these results were obtained even though mood did not influence performance and decision-related ERP responses (i.e., P300) to the centrally presented visual stimuli, suggesting that an enhanced level of positive affect had primarily an

influence on covert attention allocation towards peripheral (unattended), as opposed to central (attended) stimuli. We discuss the implications of these new findings below.

Positive emotion broadens attention

In order to assess the influence of positive mood on attentional processes, participants were randomly assigned to either a positive or neutral MIP. Given that this MIP consists of self-relevant imagery and music, the observed changes in positive affect may be attributed to the modulation of higher-level cognitive or affective processes, as opposed to mere phasic reward (Hickey, Chelazzi, & Theeuwes, 2010; Kringelbach & Rolls, 2004; Pessoa & Engelmann, 2010; Rolls, 2000; Van Steenbergen et al., 2009) or the selective induction of approach-motivated affect (Gable & Harmon-Jones, 2008, 2010). In contrast, the novel MIP we used rather elicited a positive mood characterized by low intensity in approach motivation, since the emotions evoked were not relevant in terms of any specific (task) goal³. The results of the manipulation check showed that the MIP was successful in increasing subjective feelings of positive mood, selectively in the positive mood group. However, manipulation check did not include complementary measures of arousal. Hence, it is possible that not only positive valence, but also arousal accounted for changes in attention control processes following the induction of positive mood in our study. Consistent with previous research (Ashby et al., 1999), we surmise that this change in positive mood following the MIP may be associated with a sustained increase in dopaminergic levels in specific cortical and subcortical structures, related to executive functions. Nonetheless, it remains unclear at this stage whether the

³Our results suggest that non-verbal VASs may be more sensitive than the PANAS to capture subtle changes in positive mood (Rossi & Pourtois, 2011), given that in Experiment 2, pre-post change in mood was only found with the VASs. As the change in affective state after our MIP is mild, such a change might be better captured by an instrument that can pick up small variations along a continuous scale (cf. VAS), as opposed to a limited number of discrete categories (cf. PANAS). Moreover, the presence of verbal labels for the PANAS may prevent participants from deviating substantially in their estimations in a repeated measures design. Moreover, the positive affect scale of the PANAS is principally measuring ‘positively valenced affects’ (Watson, Wiese, Vaidya, & Tellegen, 1999), high in activation (Russell & Carroll, 1999) and how much the participant enjoys engaging with his/her environment (Crawford & Henry, 2004). By contrast, the VASs we used in this study assess current positive feelings regardless of their origin/nature and independently from the level of activation they may elicit. Given the individualization of our MIP, the general scope of the VASs might be better suited than the PANAS in order to capture subtle changes in mood.

elected positive MIP actually yielded either phasic or tonic changes of dopamine levels in targeted prefrontal regions.

Previous studies already showed that changes in positive mood are related to changes in cognitive functions, including the use of a more open (Estrada et al., 1997), creative (Isen et al., 1987), integrative (Isen et al., 1991) or flexible (Isen & Daubman, 1984) thinking style. Taken together, these results point to a role of positive affective states as being able to trigger a broadening of the attentional scope (Derryberry & Reed, 1994). Based on this evidence, Fredrickson and colleagues (Fredrickson, 2001; Fredrickson & Levenson, 1998) advocated in the broaden-and-build theory that negative mood would prompt a narrowing of thought-action tendencies and attentional focus, while positive mood would on the contrary broaden people's thought-action repertoires and attentional scope. This way, mood provides human organisms with an adaptive and flexible mechanism enabling to efficiently cope with changing environmental demands, by dynamically modulating the way incoming information is processed and eventually stored in memory systems (Gray, 2004).

However, the evidence showing that positive affect can trigger a genuine broadening of the visual attentional scope and induce a more global information processing style is scarce. Previous studies used mainly cognitive control or interference tasks, such as the flanker task (Rowe et al., 2007). Rowe and colleagues (2007) found that in positive mood, flankers had a greater interference effect on central task-relevant stimuli relative to neutral and sad mood, even when the spacing between target and flankers was increased. This broadening effect seems to be related to changes in the extrastriate visual cortex, at the level of the P1 (Moriya & Nittono, 2011). These results show an increased proneness to distraction and are consistent with a broadened attention in positive mood (Fredrickson, 2001; Fredrickson & Levenson, 1998), even though a direct link between positive mood and changes in attention control mechanisms remains difficult to establish, based on these studies.

Because these interference tasks primarily rely on several cognitive processes beyond attention (e.g. executive functions and cognitive control, see Botvinick, Braver, Barch, Carter, & Cohen, 2001), it is unclear whether positive mood can causally lead to a change in the attention focus and in turn gate early sensory stimulus processing. Therefore, the main goal of our study was to address this question using a standard visuo-spatial task (Rauss et al., 2009; Rauss et al., 2011; Rossi & Pourtois, 2012; Schwartz et al., 2005), capitalizing on the high temporal resolution provided by ERPs to track attention-dependent changes in early sensory processing triggered by the earlier induction of a positive mood.

Neurophysiological mechanism underlying broadening of attention

Participants were asked to perform a demanding oddball detection task at fixation, ensuring that voluntary attention was properly locked to this position in the visual field, but leaving enough attentional resources available for the covert processing of visual distractors (EEG experiment) or overt processing of exogenous task-relevant visual textures (behavioral experiment). These uniform visual textures were briefly flashed in the upper visual field at an unpredictable time and variable location. Using ERP measurements, we could thus track electrical brain activity unambiguously elicited either by the central or peripheral stimuli, and assess at which stage their respective sensory processing was modulated by the induction of positive mood. We reasoned that if positive mood truly broadens attention scope, then the sensory processing of the unattended peripheral distractors should be altered, especially for the unattended stimuli shown at the most extreme spatial location relative to fixation.

Our new ERP results confirm this conjecture and show that the earliest stage of stimulus processing in V1, as indexed by the C1, is influenced by the location of the distractor in the upper visual field, as well as by mood. The amplitude and polarity of the C1 systematically varies with the position of the stimulus in the visual field, reflecting an early retinotopic encoding effect (Clark et al., 1995). Using a standard ERP topographic mapping

analysis (Pourtois et al., 2008), we found that in a neutral mood, participants showed a non-linear reduction of the topographical C1 component with increasing distance between the distractor and fixation, reflecting the spatial sensitivity of the C1 (Clark et al., 1995). However, participants in the positive mood group did not show such a spatial gradient effect. Hence, the spatial gradient of the C1 found in the neutral mood group was blurred after the induction of positive mood, showing a drop in selectivity for the early spatial encoding of distractors in V1. These findings show an interaction effect between bottom-up sensory processing, guided by low level stimulus information (Egeth & Yantis, 1997; Wolfe & Horowitz, 2004), in this case the spatial location of the distractor stimulus shown in the upper visual field (Rauss et al., 2011) and top-down factors (Buschman & Miller, 2007; Corbetta & Shulman, 2002; Marois & Ivanoff, 2005; Theeuwes, 2010) such as the current mood state of the participant (Gray, 2004; Rossi & Pourtois, 2012).

Of note, we found that this effect of mood on early sensory processing of the distractors was task-specific, mood dependent and selective for the C1 component. During the localizer, we found that the C1 component to these same peripheral distractors was not influenced anymore by mood, although the electrophysiological properties of the C1 were very similar in the main attention task and localizer (see Figure 6). This might be explained by mood effects fading out during the recording of the localizer blocks and/or the task differences between the localizer (i.e. passive viewing conditions) and the main task blocks. In this sense, the absence of mood effects on the localizer blocks might indicate a specific effect of positive mood on active filtering of irrelevant information, instead of an aspecific influence of this factor on the mere early bottom up processing of visual stimuli in V1. However, future studies are needed to assess and better characterize (short scale) time-dependent fluctuations of effects of (positive) mood, and how they may influence early visual and attention brain processes (including the C1 component). More specifically, whether

positive mood alters spatial properties selectively or feature-based components of (selective) attention (or both) requires additional empirical validation. Likewise, given the existing evidence showing opposite effects of positive vs. negative mood on the global vs. local information processing style (Gable & Harmon-Jones, 2008, 2010; Gasper & Clore, 2002; Rowe et al., 2007), additional work is needed as well in order to assess whether positive mood primarily influences the information processing style overall, or instead, is best characterized by process-specific changes concerning attention control mechanisms.

Unlike the C1 component, analyses of the extrastriate P1 component (Hillyard & Anllo-Vento, 1998; Martinez et al., 1999) failed to reveal any change as a function of stimulus position in the upper visual field, consistent with previous ERP findings (Clark et al., 1995). Likewise, mood had no effect on the topographical properties of the P1 component. However, given the strong anatomical connections between the prefrontal cortex and the parietal and occipital cortices, a modulatory effect of positive mood remotely influencing not only early visual areas (including V1), but also the extrastriate visual cortex (and hence the P1 component) appears more likely. Moreover, our observation of a C1-selective effect of the positive mood could also be explained by the specific task demands and stimulus parameters used in our study. The elected experimental paradigm likely promoted attention competition/selection primarily in the spatial domain (see also Rossi & Pourtois, 2012). We surmise that a modulation of the P1 component by (positive) mood could also be found if different task demands and stimulus characteristics would be used, for example dot probe or cueing tasks (see Pourtois, Grandjean, Sander, & Vuilleumier, 2004).

Another important finding of our study was to show that mood did not change the processing of the centrally presented/task-relevant stimuli, in both experiments. As expected, the amplitude of the P300 component was strongly influenced by task demands (Kim et al., 2008; Kok, 2001; McCarthy & Donchin, 1981; Sawaki & Katayama, 2007), being larger for

perceived (deviant) targets than for standards. However, this effect was not different between the two mood groups, in agreement with earlier ERP studies (Moriya & Nittono, 2011; Rossi & Pourtois, 2012). Moriya and Nittono (2011) used a flanker task, but they did not report any reliable effect of either positive or negative mood on the amplitude of the P300 component. They concluded that attention might only be influenced by mood at early stages of stimulus processing, as opposed to response selection and decision processes. Rossi and Pourtois (2012) also confirmed that neither positive nor negative mood influenced the amplitude of the target-related P300 component (as well as accuracy at the behavioral level), using an adapted version of the experimental paradigm used in this study. In their ERP study, participants were instructed to attend to a RSVP at fixation, consisting of the same line segments as in the current study. In some trials, a deviant line orientation was presented and these deviant lines had to be detected by participants (ratio standard-target line orientations was 4:1). Perceptual load for these central stimuli was manipulated in this study, such that the detection task could be easy, intermediate or difficult. Participants performed this task under either a positive or a negative affective state (within-subject design). Results showed that the target-related P300 component, as well as accuracy at the behavioral level, varied strongly and in a predictive direction depending on task difficulty. However and importantly, mood did not interact with these effects, including for the easiest and most difficult level of task difficulty. By contrast (and similarly to the present study), in this earlier study mood altered the early visual processing of (unattended) peripheral distractors, suggesting that (state-dependent) affect mainly influenced peripheral (and unattended stimuli) as opposed to central vision (and the processing of attended stimuli). The new ERP results presented in this study (see Experiment 1) are compatible with this interpretation and they confirmed an asymmetry between central/attended and peripheral/unattended locations for effects of mood or affect on (early) visual perception. In contrast, another study did find a modulation of the P300 component by

negative affective state (threat of shock, Shackman et al., 2011). Hence, it remains unclear if the decision-related P300 component can be modulated by affective state. More generally, our results suggest that positive mood may lead to qualitatively different effects during sensory processing and decision making processes for task-relevant stimuli, relative to negative emotions. Future ERP studies comparing more directly effects of positive vs. negative mood are needed in order to assess whether not only early sensory processing stages (e.g. C1 component), but also later decision-related processes are equally influenced by these opposite affective states or not. Likewise, it appears necessary to explore further the likely dependency of some of these ERP components to specific neurotransmitter systems. In particular, given that positive mood is thought to be mediated by specific dopaminergic systems (Ashby et al., 1999), some of the present ERP effects could tentatively be related to changes in these dopaminergic systems. In this regard, studies linking the P300 component either to dopaminergic (see Pogarell et al., 2011) or adrenergic inputs (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Polich, 2007) provide important hints on the actual organization of the underlying brain architecture and neural systems mediating effects of (positive) mood on attention.

More generally, our findings suggest that effects of positive mood were specific to the processing of the peripheral, task-irrelevant stimuli and they did not influence task-relevant, central stimuli. This result allows us to rule out the possibility that changes in early sensory processing at the level of the C1 for the peripheral visual textures were explained by systematic behavioral performance imbalances between mood groups for the task at fixation. The behavioral data collected during the EEG experiment and the additional behavioral experiment, showing no difference in accuracy nor in RTs between mood groups for the task at fixation, further support this conclusion.

Additional information regarding the nature and extent of the selective change produced by positive mood was provided by the additional behavioral experiment. We reasoned that if the effect of positive mood may correspond to a drop in early spatial encoding selectivity, as our new ERP results for the C1 suggest, the capacity to discriminate subtle geometric differences between different peripheral stimuli may be impaired in positive mood, compared to neutral mood, given the intrinsic attention competition exerted by the three non-overlapping spatial positions in the upper visual field. This new result is compatible with earlier findings in the literature, showing that a larger attentional scope may lead to an associated loss in processing efficiency and spatial resolution (as compared to a smaller scope; Castiello & Umiltà, 1990, 1992; Eriksen & Yeh, 1985) and that this is reflected in a decreased neural signal change in the corresponding retinotopic area (Muller et al., 2003). These results provide support for the assumption of a trade-off effect between the size of the attentional focus and the efficiency/resolution of visual (spatial) processing (Castiello & Umiltà, 1990, 1992; Eriksen & Yeh, 1985; Ivry & Robertson, 1998; Muller et al., 2003). In line with this reasoning, when peripheral textures became task-relevant and had to be discriminated (Experiment 2), accuracy dropped as a function of the distance of the textures relative to fixation. Similarly to these previous findings showing a drop in efficiency of stimulus processing when the attentional scope was broadened, we found that participants in the positive mood group committed on average substantially more discrimination errors than participants in the neutral mood group across the three positions. Combined together with our new C1 results showing an altered sensitivity between the three positions in the upper visual field in positive relative to neutral mood (Experiment 1), this decrease in accuracy in the positive mood group might suggest a drop in attention selectivity across these three positions in the upper visual field (Experiment 2). However, some caution is needed when comparing directly the results of both experiments, given that they differ along several dimensions.

While working memory is presumably taxed similarly in both experiments by the central RSVP, in Experiment 2 peripheral textures were also task-relevant and required an explicit visual discrimination, possibly triggering a more open attention focus compared to the task-irrelevant distractors in Experiment 1. Moreover, if we assume a general limited resources account for attention capacities (see Marois & Ivanoff, 2005), then increasing task demands may block or dampen effects of (positive) mood on early visual perception. Nonetheless, in Experiment 1, we found clear evidence for an effect of position of textures in the upper peripheral visual field at the level of the C1, indicative of a change in the distribution of spatial attention in this portion of the visual field, as well as a significant modulation of this effect by the positive mood. Future studies are needed to assess whether task-relevance of peripheral textures reliably influences the size and extent of positive mood effects (on early visual perception). The results of this study (Experiment 2) show that despite a dual task setting and a (high) working memory load, positive mood could still exert a modulatory effect on the ability to discriminate peripheral textures shown in the upper visual field, an effect which presumably arises early following stimulus onset in the primary visual cortex when the location of these textures were precisely/retinotopically encoded (see results of Experiment 1).

Presumably, if positive emotion broadens attention, the distractor or location specificity may be impaired because attention is by definition operating over a potentially more expanded region. Changes in dopaminergic-dependent prefrontal attention control mechanisms under positive mood could underlie these early visual perception effects (Ashby et al., 1999; Lavie, 1995). However, the actual mechanism linking positive mood, dopamine, and cognitive processes is not yet fully understood, partly due to the existence of several dopamine receptor types and different dopaminergic-dependent neuromodulation pathways, connecting to different (sub)cortical brain regions. It is likely that the influence of sustained

positive mood (as achieved in this study) on specific cognitive processes, such as attention, actually concerns tonic changes in dopamine levels, as opposed to mere phasic fluctuations. Alternatively, it has been suggested that phasic dopamine increases in prefrontal cortex, elicited by stimuli that are rewarding or reward-predicting, serve as a pervasive gating signal. Accordingly, we surmise that the positive MIP, instructing participants to focus on a personal experience of positive mood, served as a reward cue for the participants, hence likely influencing the phasic dopamine release in this region, even though future studies are needed to corroborate this conclusion.

Broadening through decreased inhibition?

The alteration in early sensory processing of the distractors under positive mood (and its behavioral effect) might be explained by a change in higher-level attention control mechanisms (Corbetta & Shulman, 2002; Lavie, 2005). It is possible that resources left over and not consumed by the main oddball task at fixation may be used to process covertly these peripheral stimuli (Lavie, 1995, 2005; Lavie et al., 2004; Lavie & Tsal, 1994), and this effect could be exacerbated under positive mood. Hence, positive mood may not influence sensory processing in V1 directly, but rather (tonically) loosen the normal top-down control exerted by prefrontal attention control regions onto V1 (see also Rossi & Pourtois, 2012). Therefore, the effect of positive mood in our study might very well operate at this level and interfere with the normal recruitment of prefrontal cognitive control regions aimed at downplaying the distraction effect induced by these peripheral visual textures. These prefrontal regions primarily include the dorsolateral prefrontal cortex (Miller & Cohen, 2001; Posner & Presti, 1987), as well as the anterior cingulate cortex (Posner & Petersen, 1990; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuiss, 2004). Interestingly, because both regions are receiving strong dopaminergic inputs from the midbrain and basal ganglia, and because positive mood may be associated with a tonic change in these dopaminergic brain systems (Ashby et al.,

1999), the observed changes in V1 after the induction of positive mood in our study may tentatively be linked to these distant prefrontal effects, or alternatively to a more global change in the fronto-parietal network supporting the endogenous control of attention (Corbetta & Shulman, 2002). In other words, positive mood might affect these prefrontal inhibitory systems (Wang et al., 2011), eventually leading to a change in early sensory processing in V1, given the strong anatomical projections from these prefrontal areas to early sensory cortices, including V1 (Van Essen, Anderson, & Felleman, 1992). Hence, because of this decreased prefrontal control or inhibitory mechanism, positive emotion alters the early sensory processing in V1, and hence the attention selectivity, revealing in turn a downside of positive emotion on early visual cognition (see also the results of the behavioral experiment corroborating this conclusion). One may assume that a similar release in prefrontal inhibitory control may explain a variety of effects observed under positive mood, including a more global (as opposed to local) processing style (Gable & Harmon-Jones, 2010), a higher susceptibility to distraction during interference tasks (Rowe et al., 2007), a lower adaptation following conflict detection (Van Steenbergen et al., 2010), as well as eventually an enhanced creative style (Isen, 2000; Isen & Daubman, 1984; Isen et al., 1987; Isen et al., 1991). However, it should be mentioned that the focus of our study was on how “low-level” attentional and visual processes could be modulated by (transient and short-lived) changes in levels of positive mood, as opposed to alterations of high-level cognitive functions, such as creativity, reasoning, problem solving or language. Interestingly, it is plausible to assume that a common “basic” process might underlie changes seen in a broad range of cognitive functions after the induction of positive emotion. More specifically, a substantial decrease in frontal inhibitory processes following the induction of positive mood, such as postulated in earlier research or models (Rowe et al., 2007, Biss & Hasher, 2011; Biss et al., 2010), might possibly explain, although indirectly, the present ERP results, as well as a wide range of

behavioral phenomena previously reported in the literature, including the adoption of a more creative and flexible information processing style. Additional brain-imaging studies are needed, however, to link more directly changes in such prefrontal inhibitory control mechanisms with the induction of positive mood, and finally try to causally relate these putative changes in higher prefrontal brain regions with specific alterations during early sensory processing or attention control, as revealed in our study.

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Figures legend

Figure 1. Task. (a) Visual textures were briefly presented in random order at one out of three possible locations in the upper visual field: close to fixation, at medium distance or far from fixation. These textures had to be ignored during the EEG experiment, but were task-relevant in the behavioral experiment. In this case, participants were asked to judge whether the elements forming each texture were either quadratic or rectangles, while keeping fixation in the center of the screen. (b) The main task at fixation (shared across the two experiments) consisted of an oddball line orientation task. Participants were asked to detect covertly (EEG experiment) or overtly (behavioral experiment) deviant line orientations embedded in a RSVP at fixation. Standard lines were tilted 35° counterclockwise, while deviant lines were tilted 45° in the same direction. The ratio between standard and target orientations was 4:1. The fixation cross after the line stimulus was shown for 250-500 ms in the EEG experiment and for 500-750 ms in the behavioral experiment. In half of the trials (random order), a visual texture was briefly presented (250 ms) at one out of three positions in the upper visual field, at a variable time following the presentation of the central line. In the other half, no texture was presented. Hence, the appearance and actual location of the visual textures were unpredictable, and their presentations never overlapped with the centrally presented lines

appearing on the screen roughly every 775 ms in the EEG experiment, and every 1025 ms in the behavioral experiment. (c) Half of the peripheral textures were made up by one type of quadrangle elements (0,5 cm wide x 0,4 cm high), whereas the other half had slightly different quadrangle elements (0,6 cm wide x 0,3 cm high), with an equal number of presentations of each type for each of the three locations.

Figure 2. Evolution of levels of positive mood across the four (consecutive) measurement points, separately for the positive mood group (dark grey line) and the neutral mood group (light grey line). Mean scores (with 1 S.E.M as error bar) for the happy VAS (upper panel) and pleasant VAS (lower panel) are presented for (a) Experiment 1 and (b) Experiment 2. For Experiment 2, results are shown for all 35 participants (continuous line) vs. 28 participants (14 per group) showing clear effects of mood depending on the MIP (dotted line; see footnote 2 on p. 22).

Figure 3. (a) Accuracy rates for the identification of peripheral textures (Experiment 2) show a decrease in accuracy with increasing distance from fixation (C/close to fixation; M/medium position; F/far from fixation). However, an overall lower accuracy in the positive mood group (dark grey) relative to the neutral mood group (light grey) was found (* $p < 0.05$; black bars represent standard errors of the means). (b) Accuracy rates for the oddball line orientation task at fixation for the EEG experiment (left panel). Trials for which participants correctly detected a target (or correctly rejected a non-target) were counted and these numbers were then converted to percentages (bearing in mind that in total 300 trials were presented). Results for the behavioral experiment (right panel). In each experiment, no accuracy difference was found between the positive (P) and neutral (N) mood group.

Figure 4. Grand average ERPs to standard (solid) vs. target (dashed lines) central stimuli at a representative midline electrode (POz). A clear P300 was present for target line orientations (dashed line) in the neutral (grey) and positive (green) mood group, whereas this decision-

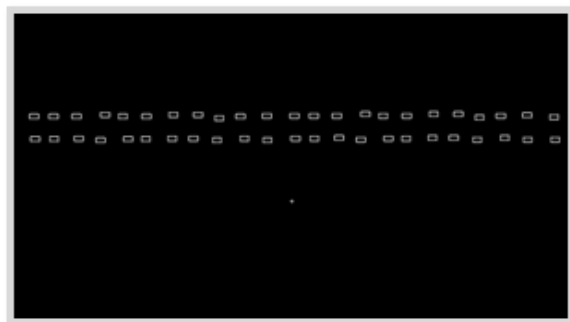
related component was strongly attenuated for standard line orientations (solid line). This conspicuous P300 effect reflecting attention allocation to the target stimuli was similar for the neutral and positive mood groups (see text for numerical values). Topographical voltage maps (back view) for the P300 component (computed during the 400-600 ms post-stimulus onset) are shown for the 2 conditions and 2 groups, separately.

Figure 5. (a) Results of the topographical ERP mapping analysis (EEG experiment). This analysis identified a main cluster (88-127 ms post-stimulus onset for position close) corresponding to the striate C1 component, followed by another one corresponding to the extrastriate P1 component (141-186 ms post-stimulus onset for position close). Whereas the topography of the C1 substantially changed with the position (C/close; M/medium; F/far) of the (unattended) textures in the upper visual field, the configuration of the electric field of the P1 did not (see results section for numerical values). The corresponding voltage maps (back view) are shown. Following standard practice, amplitude differences were normalized (i.e. the amplitude value at each electrode was divided by the global field power - GFP). (b) Grand average ERPs at electrode POz to visual textures, separately for each group (either positive/green or neutral/grey mood) and each position (close/solid lines; medium/dashed lines; far/dotes lines) in the upper visual field. As waited, the amplitude of the C1 substantially varied as a function of the position of the textures in the upper visual field (being smaller for far relative to close position), but this effect was stronger for participants in a neutral mood (left panel), compared to a positive mood (right panel). (c) Results (* $p < 0.05$; black bars represent standard errors of the means) of the back-fitting (see methods) of the dominant C1 topography [see blue frame in (a)]. Whereas the GEV/goodness of fit of the dominant C1 topography sharply decreased for the medium or far, relative to the close position in the neutral mood group (left panel), suggesting a normal spatial gradient effect, this effect was not seen in the positive mood group (right panel) where C1 activity for the far

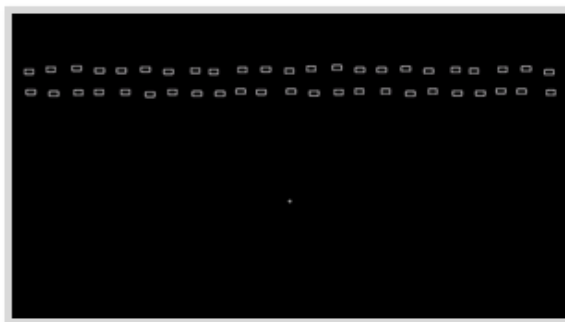
(or medium) position was not significantly lower than for the close position (see results section for numerical values).

Figure 6. Results of the localizer. Grand average ERPs at electrode POz to peripheral visual textures presented close to fixation, separately for the upper (blue line) and lower visual field (red line) (a) for the neutral mood group and (b) for the positive mood group. These ERPs confirm that in both groups a diagnostic C1 polarity reversal was equally present, early on following stimulus onset over occipito-parietal electrodes along the midline, for visual stimulations in the upper vs. lower visual field, consistent with the electrophysiological signature of this early retinotopic visual component (Rauss, et al., 2009). The corresponding voltage maps (back view) are shown. Maps show normalized amplitude differences (i.e. the amplitude value at each electrode was divided by the GFP).

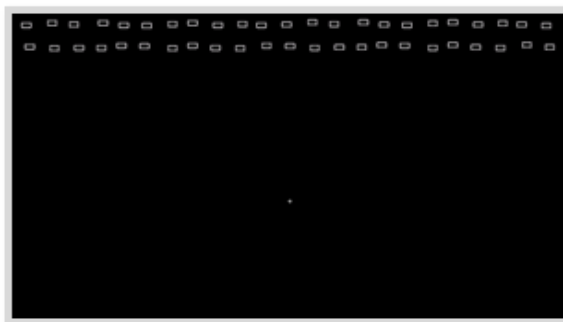
(a)



Close

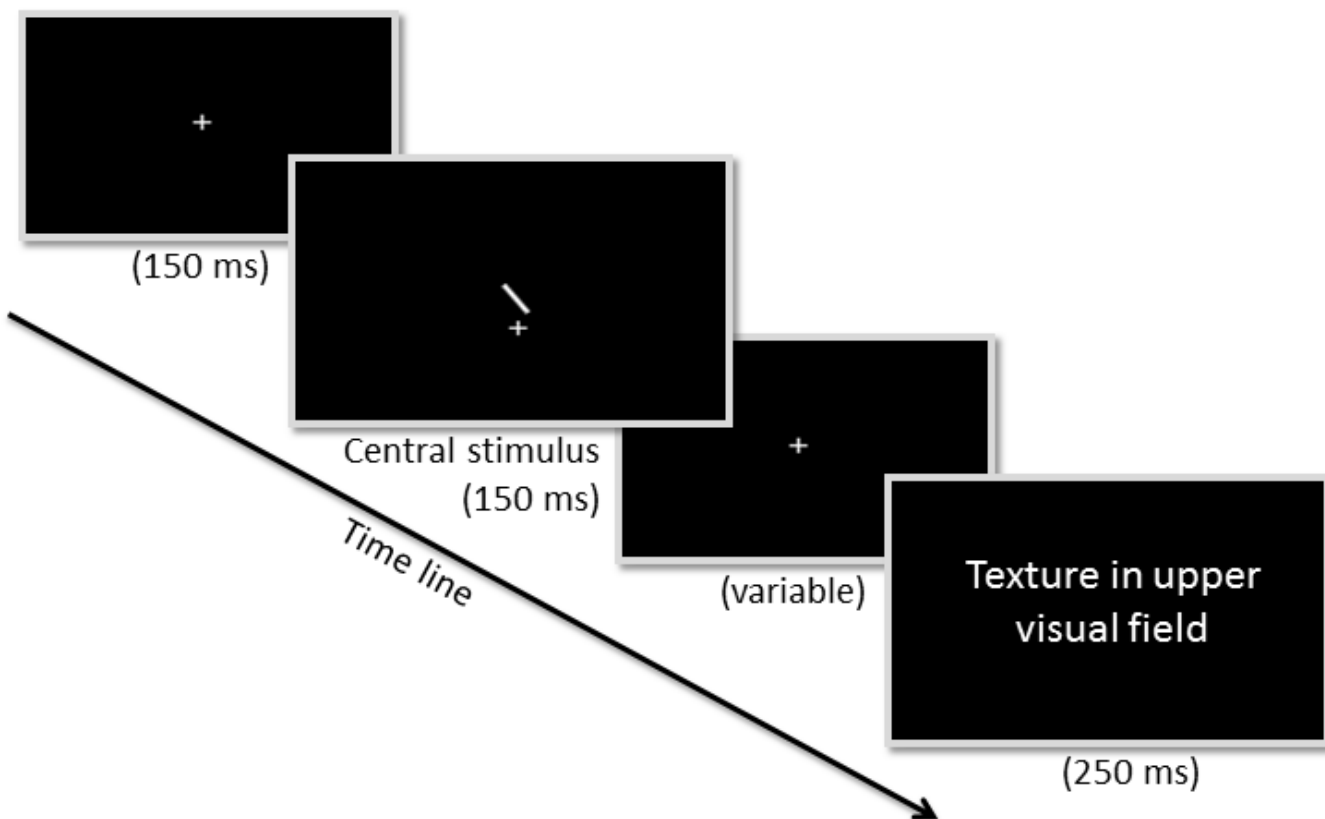


Medium

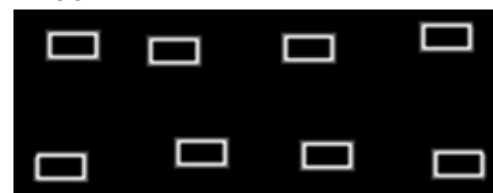


Far

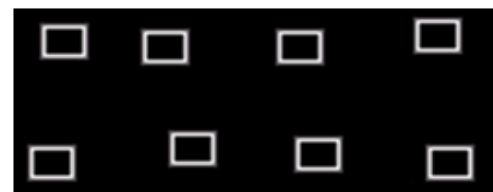
(b)

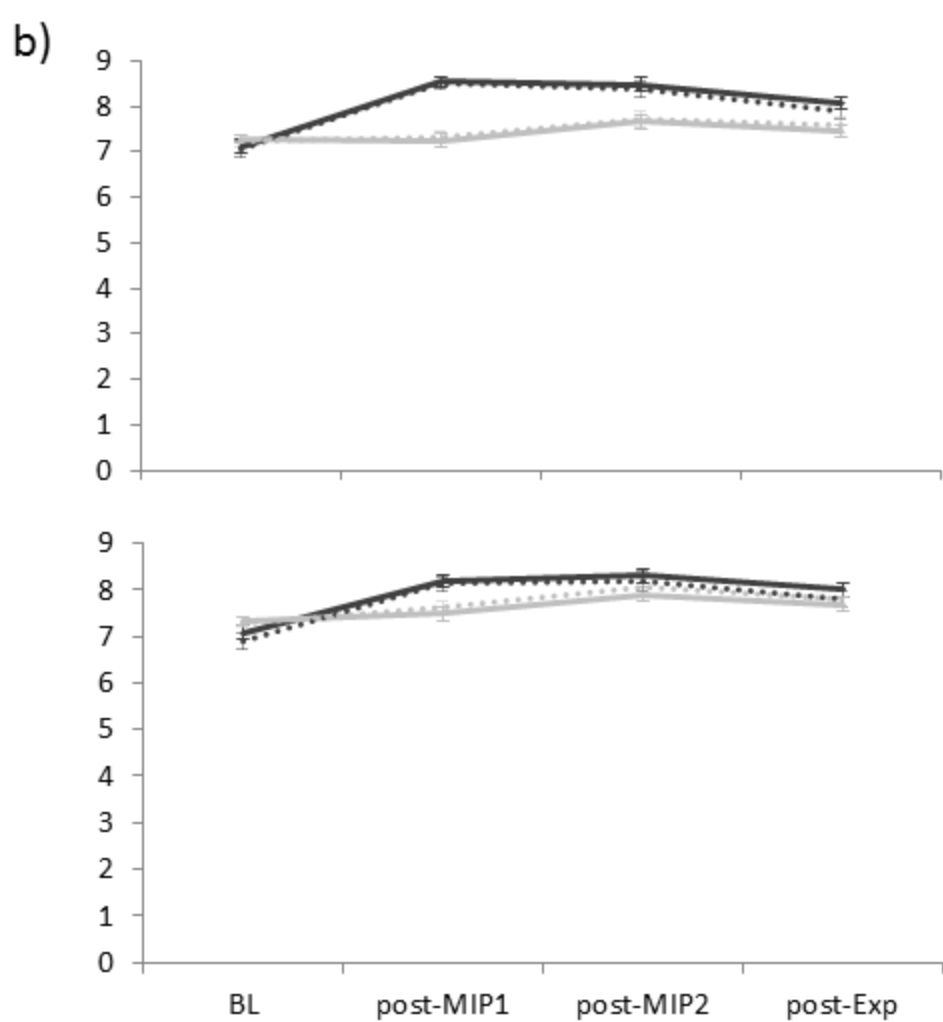
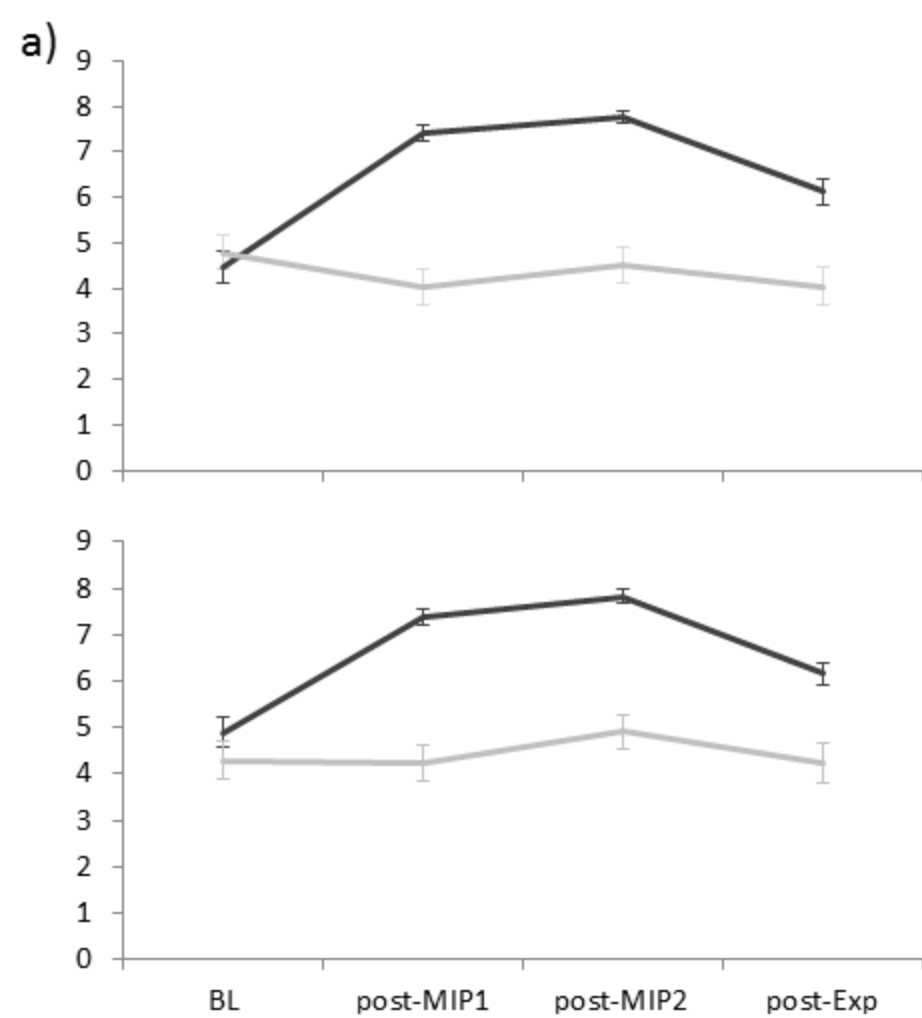


(c) Type 1

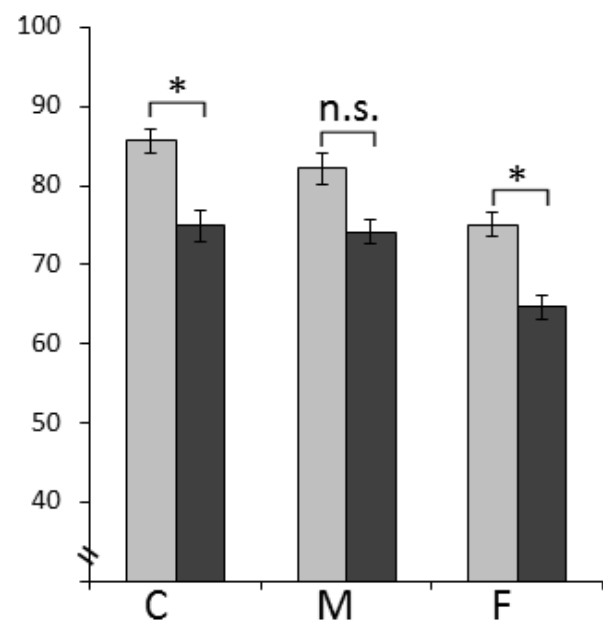


Type 2





(a)



(b)

