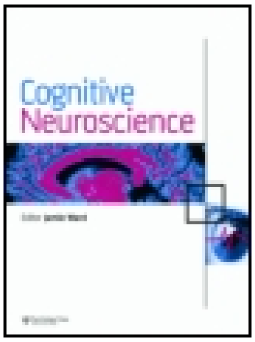

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ARTICLE

Early retinotopic responses to violations of emotion–location associations may depend on conscious awareness

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ABSTRACT

Reports of modulations of early visual processing suggest that retinotopic visual cortex may actively predict upcoming stimuli. We tested this idea by showing healthy human participants images of human faces at fixation, with different emotional expressions predicting stimuli in either the upper or the lower visual field. On infrequent test trials, emotional faces were followed by combined stimulation of upper and lower visual fields, thus violating previously established associations. Results showed no effects of such violations at the level of the retinotopic C1 of the visual evoked potential over the full sample. However, when separating participants who became aware of these associations from those who did not, we observed significant group differences during extrastriate processing of emotional faces, with inverse solution results indicating stronger activity in unaware subjects throughout the ventral visual stream. Moreover, within-group comparisons showed that the same peripheral stimuli elicited differential activity patterns during the C1 interval, depending on which stimulus elements were predictable. This effect was selectively observed in manipulation-aware subjects. Our results provide preliminary evidence for the notion that early visual processing stages implement predictions of upcoming events. They also point to conscious awareness as a moderator of predictive coding.

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C1; EEG; vision; visual evoked potentials

Introduction

Over the last 25 years, there has been a steady increase in studies showing a surprising degree of flexibility in low-level sensory cortices in the adult brain. Initially, research on perceptual learning demonstrated long-lasting and highly specific training effects on behavioral performance (Karni & Sagi, 1991). Such changes in behavior were later linked to equally specific modulations of neural activity as measured with functional magnetic resonance imaging (Schwartz, Maquet, & Frith, 2002). One crucial question is whether such plasticity reflects changes intrinsic to low-level sensory cortices (Gilbert, Sigman, & Crist, 2001), or whether it is primarily due to high-level control signals that shape later processing stages (Roelfsema, Lamme, & Spekreijse, 1998), or a combination of both factors (Muckli & Petro, 2013). Recent findings (Bao, Yang, Rios, He, & Engel, 2010), including our own (Pourtois, Rauss, Vuilleumier, & Schwartz, 2008), seem to favor the first alternative: namely, that even the earliest stages of processing in low-level sensory cortices are affected by learning, corresponding to either structural modifications within these areas (Dorjee & Bowers, 2012; Rauss & Schwartz, 2012) or very early effects of high-level control signals (Li, Piëch, & Gilbert, 2004).

These findings have been extended to shorter timescales, with a number of studies indicating that early visual processing can be modified online, i.e., without extensive training procedures, by directing spatial attention to the periphery (Kelly, Gomez-Ramirez, & Foxe, 2008; Poghosyan & Ioannides, 2008) or withdrawing it via attentional load (Rauss, Pourtois, Vuilleumier, & Schwartz, 2009, 2012a). We have proposed a model that explains such effects in terms of predictive coding (Rauss, Schwartz, & Pourtois, 2011). However, others have not been able to replicate these findings (Ding, Martinez, Qu, & Hillyard, 2014; Fu, Fedota, Greenwood, & Parasuraman, 2010), and there is a continuing debate concerning this discrepancy (Rauss, Pourtois, Vuilleumier, & Schwartz, 2012b).

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A central argument on which we based our model (Rauss et al., 2011) was that the type and extent of predictability afforded by different experimental protocols seems closely linked to whether or not top-down effects on early visual processing are observed. More specifically, it appears that top-down effects have only been found when attention can be focused on or withdrawn from predefined regions of space without affecting task performance (Kelly et al., 2008; Rauss et al., 2009). In contrast, whenever moment-to-moment monitoring of entire stimulus arrangements is required for adequate performance, visual processing is affected only during later intervals (Roelfsema et al., 1998). Furthermore, we have argued that the increasing influence of top-down processes at higher levels of the visual hierarchy (Schwartz et al., 2005) is due to a lack of stimulus-specific, long-range feedback connections to primary visual cortex in particular (Nienborg & Cumming, 2014).

Against this background, the present study sought to test the hypothesis that even the earliest phases of visual processing reflect basic principles of predictive coding (Kok, Jehee, & Lange, 2012; Schröger, Marzecová, & Sanmiguel, 2015; Summerfield & Egner, 2016). Our aim was to test whether mismatches between predictions based on previously learned stimulus associations and actual stimulation would result in retinotopically specific error signals that can be detected with scalp electroencephalography (EEG).

In most of the human EEG studies reviewed above, the main indicator for early visual cortex activity has been the so-called C1 (Jeffreys & Axford, 1972; Rauss et al., 2011). The C1 represents the first component of the visual evoked potential (VEP) in humans, with an onset latency of around 50 ms post-stimulus and a peak latency that is usually below 100 ms. In addition to its early timecourse, the C1 shows a characteristic inversion of polarity, with positive voltages observed following stimulation restricted to the lower visual field, and negative voltages after stimulation restricted to the upper visual field. Jeffreys and Axford (1972) argued that the combination of these characteristics indicates that the component's main neural sources are located in the primary visual cortex (V1). This conclusion has been supported by numerous studies using different EEG source localization methods (Capilla et al., 2016; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Martínez et al., 1999; Pourtois et al., 2008). More recently, studies using individually tailored distributed inverse solutions have cast doubts on the extent of V1 involvement in generating the C1 (J. M. Ales, Yates, & Norcia, 2010), leading to renewed interest and intense discussion on how to assess early visual processing in humans (J. M. Ales, Yates, & Norcia, 2013; Kelly, Schroeder, & Lalor, 2013; Kelly, Vanegas, Schroeder, & Lalor, 2013).

Notwithstanding these issues, the C1 does represent the earliest reliable handle on cortical visual processing in humans, and we therefore tested our hypothesis on this particular component. To do so, we had healthy human participants watch a stream of centrally presented images of human faces showing either happy or fearful expressions. On frequent learning trials, each type of expression was always followed by arrays of high-contrast line-elements restricted to either the upper or lower visual field (counterbalanced across participants). On infrequent test trials, faces with either expression were followed by stimuli in both the upper and the lower visual field.

Our results indicate no systematic, polarity-specific shifts in C1 amplitude as a function of stimulus expectations across our full sample. However, exploratory analyses suggest that awareness of emotion–location associations is associated with decreased P1 responses to images of emotional faces, as well as increased early visual cortex responses to unexpected peripheral stimulation.

Methods

Participants

A total of 21 subjects were tested. All subjects were right-handed, had normal or corrected-to-normal vision, and none of them reported any history of psychiatric or neurological disorders. Written informed consent was obtained prior to screening for exclusion criteria and the study was approved by the local ethics committees at Ghent University and the University of Tübingen. Two subjects had to be excluded, one due to poor EEG data quality and one due to poor behavioral performance. The remaining 19 subjects were aged between 18 and 39 years; 15 were female.

Stimuli

All stimuli were shown against black background on a 19 in cathode ray tube screen (resolution 1024 × 768 pixels; refresh rate 60 Hz) at a viewing distance of 57 cm using Presentation, Version 16.1 (Neurobehavioral Systems, Inc., Albany, CA, USA). Trials started with a white central fixation cross shown for 500 ms. This was followed by a centrally presented grayscale image of a human face expressing different emotions (approximately 3.2 × 4.6° of visual angle) shown for 200 ms. Sixteen images were taken from the Ekman set (Ekman & Friesen, 1976), with eight different individuals (four male, four female) expressing either happiness or fear.

For the main experimental task, peripheral arrays of white line elements were presented in addition to the central face image after 200 ms, either in the upper visual field (UP), the lower visual field (LO), or both upper and lower visual fields (full-field, FULL). Peripheral stimuli were similar to those used in previous experiments (Rauss et al., 2009). Individual stimuli consisted of 11 rows and 11 columns covering an area of 10.7 × 10.7°. For each trial, two (UP and LO trials) or four (FULL trials) such stimuli were randomly drawn from a pool of 10 and shown in different quadrants on the computer screen, sparing 3.6° around the horizontal meridian and 7.6° around the vertical meridian. The combined stimulus (central face plus peripheral lines) then remained on-screen for 200 ms. The interval between face and line onsets was kept constant in order to maximize the association between emotions and peripheral stimulus locations. The next trial started after an interstimulus interval randomly selected from a flat distribution between 500 and 900 ms (Figure 1).

Additional blocks contained either only central faces, only peripheral lines, or central faces with peripherally presented colored dots (see Figure 1). Basic stimulus and timing characteristics were equivalent to the main experimental task unless noted otherwise.

Design and procedure

Participants were prepared for EEG recording and seated in an electrically shielded, quiet, and dimly lit room. A chin rest was used to stabilize viewing distance at 57 cm. The experiment consisted of four types of blocks:

(1) *Main-task* blocks were used to address our central hypothesis. Subjects were instructed to ignore peripheral stimuli and focus on the

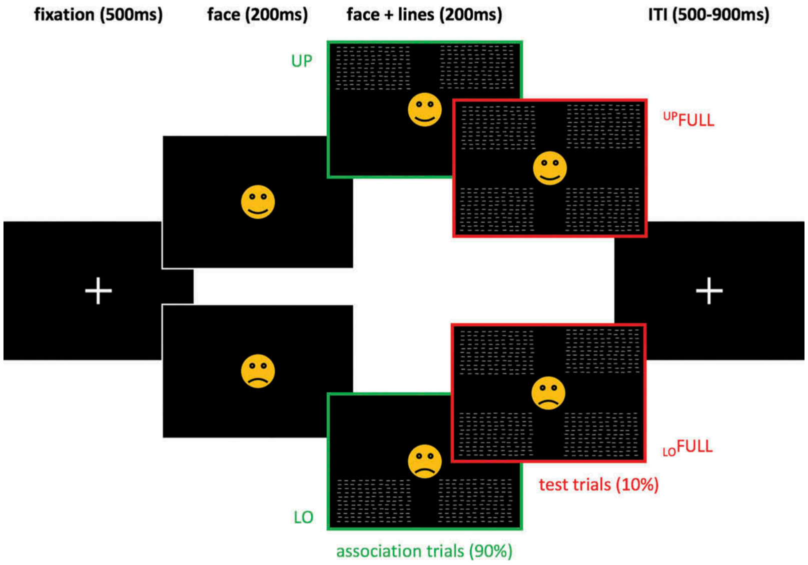

Figure 1. Stimuli and time-course for main-task trials. Emotional faces shown at fixation were accompanied by peripheral arrays of white line elements (actual stimuli were taken from Ekman & Friesen, 1976). In this example, 90% of happy faces were accompanied by lines in the upper visual field and 90% of fearful faces were accompanied by lines in the lower visual field (association trials, UP or LO, here framed in green; frames are shown for illustration only and were not part of the actual stimuli). Emotion–location associations were counterbalanced across participants. On probe trials (10%, ^{UP}FULL or $_{LO}$FULL, framed in red), faces showing either emotion were accompanied by lines in both the upper and lower visual field.

center of the screen. On 90% of trials (association trials), the position of the lines (UP vs. LO) was predicted by the emotion of the preceding face image, with face–location associations counterbalanced across participants. On the remaining 10% of trials (test trials), FULL stimuli were presented. To ensure that attention was focused on the face images, a different, pseudo-randomly selected set of 10% of trials (target trials) were followed by a response screen asking participants to indicate the emotion of the preceding face. Responses were given by pressing one of two keyboard buttons. The assignment of buttons to emotions was counterbalanced across participants.

(2) *C1 localizer* blocks were used to establish individual baseline responses to peripheral line stimuli (Rossi & Pourtois, 2012, 2014). Only peripheral line-arrays were presented in order to measure individual C1 characteristics independently of the experimental manipulations in the main task. Under passive viewing conditions, 100 stimuli were presented, with 33% UP stimuli, 33% LO stimuli, and 34% FULL stimuli shown in random order. The initial central fixation cross was presented for 700 ms to equate trial timing with the other block types.

(3) *Face localizer* blocks were used to establish individual baseline responses to centrally presented face images. Stimuli, timing, and instructions were the same as for the main task, but no peripheral stimuli were presented.

(4) *Dot-probe* blocks were used to assess behavioral learning effects. In order to measure the strength of association between emotions and visual-field locations, faces were presented centrally and a red dot was presented either in the upper or lower visual field. Subjects were instructed to respond to the position of the dot by pressing either the up-arrow or the down-arrow on the keyboard as fast and as accurately as possible.

The experiment started with a face-localizer block, followed by five main-task blocks. Then, a first dot-probe block was presented, followed by an additional five main-task blocks. Finally, a second dot-probe block and the C1 localizer block were performed. Blocks contained 100 trials and lasted approximately 3 min each. Between blocks, there was a programmed break of 30 s to avoid fatigue. After these forced break intervals, participants could initiate the next block themselves and were thus free to take longer breaks if they wished. The entire recording session consisted of 14 blocks, yielding an overall duration of approximately 50 min including breaks.

After finishing the experiment, subjects completed the Attentional Control Scale (ACS; Derryberry & Reed, 2002), the Cognitive Failures Questionnaire (Broadbent, Cooper, FitzGerald, & Parkes, 1982), and the State-Trait Anxiety Inventory (STAI) (Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983). Afterwards, they were systematically questioned concerning their awareness of any associations between centrally presented emotions and peripherally presented lines, before being debriefed and paid. Debriefing tests were included as potential covariates which might explain the expected differences in event-related potential (ERP) amplitudes. Specifically, distractibility as measured via the attention questionnaires could influence C1 amplitudes in terms of the amount of resources devoted to processing task-irrelevant stimuli in the periphery (Kelly et al., 2008; Rauss et al., 2009, 2012a); conversely, emotional reactivity could determine the amount of resources dedicated to face processing, thus limiting neural responses to subsequent peripheral stimulation; finally, conscious awareness is known to be required for certain forms of associative learning (Bekinschtein et al., 2009), and could lead to reduced prediction-error (PE) signals because unexpected stimuli are recognized as exceptions to persistent rules.

Data recording and analysis

The EEG was recorded from 128 electrodes placed according to the extended 10-10 EEG system using an elastic cap (ABC layout, BioSemi ActiveTwo System, BioSemi, Amsterdam, The Netherlands, http://www.biosemi.com). Horizontal and vertical electrooculograms were monitored using additional bipolar electrodes. Both EEG and EOG were continuously sampled at 512 Hz.

Data were processed using Brain Vision Analyzer 2 (Brain Products, Munich, Germany). During preprocessing, data were band-pass filtered between 0.1 and 40 Hz and a notch filter at 50 Hz was applied. Independent component analysis was used to correct ocular artifacts (blinks and saccades) and clearly identifiable other artifacts (e.g., heartbeat). Afterwards, all channels were re-referenced to averaged mastoids. Any remaining artifacts were rejected semiautomatically based on the following criteria: maximal allowed voltage step, 50 µV/ms; maximal voltage differences of 200 µV/200 ms; minimal/maximal allowed amplitude: −100/+100 µV; minimal voltage difference, 0.5 µV/100 ms. On average, 9.79 ± 1.19% of trials per subject and condition were excluded. Target trials (i.e., trials followed by a response screen and button press in face localizer, dot-probe, and main task blocks) were excluded from analysis. Noisy electrodes were interpolated using a fourth-order spherical-splines procedure implemented in BrainVision Analyzer. Epochs from −700 to +900 ms around the onset of peripheral stimuli were extracted. For the face-localizer data, this was achieved via additional markers in the EEG at times where peripheral lines would have occurred in the main task. Baseline correction was applied from −400 to −200 ms (corresponding to the 200 ms before the onset of face images in main-task and face-localizer blocks), in order to use the same interval without visual stimulation in all conditions.

Main task

Separate averages were computed for responses to emotional faces (fear, happy), for responses to expected peripheral line arrays (UP, LO), and for responses to unexpected peripheral line arrays (FULL). Our central hypothesis was that the latter would differ as a function of the preceding emotion and the prediction of a stimulus in either the upper or the lower visual field. Thus, additional FULL averages were computed separately for trials in which the preceding emotion was linked to subsequent UP vs. LO stimulation. We designate these as ^{UP}FULL and $_{LO}$FULL, respectively.

To quantify prediction effects on FULL responses, we performed two consecutive subtractions, both based on individual-subject ERPs. First, we obtained a cleaned estimate of visual cortex responses to peripheral stimuli. This was achieved by subtracting ERPs elicited by emotional faces in the face-localizer block from peripheral-stimulus ERPs. Since we did not observe conspicuous differences between ERPs elicited by happy or fearful faces (p = 0.75, see Results section), the average of both emotions was used for subtraction. Second, we isolated responses elicited by the predicted and unpredicted components of FULL stimuli. This was done by subtracting UP responses from ^{UP}FULL responses, and LO responses from $_{LO}$FULL responses, with all ERPs taken from the main task. We will refer to these averages as prediction-error ERPs, PE_{LO}, and PE^{UP}, as they reflect the non-subtracted stimulus component and the fact that this component could not be predicted based on the vast majority of association trials and the random presentation of infrequent test trials. As a comparison baseline for PE ERPs, we also calculated prediction ERPs by subtracting LO from ^{UP}FULL, and UP from $_{LO}$FULL. We designate these as prediction-ERPs, P^{UP} and P_{LO}, to indicate that they reflect the non-subtracted stimulus component and the fact that this component could be predicted based on the majority of association trials.

For all ERPs and subtractions described earlier, C1 peak amplitudes and latencies were measured semiautomatically based the component's distinct polarity, topographical properties, and latency, using the separate set of localizer data (see later sections). A search window between 60 and 120 ms after onset of peripheral stimuli was chosen for semiautomatic peak detection. For later components, as well as those elicited by the preceding face stimuli, amplitudes were identified for pools of electrodes determined from the grand-averages (see Figure 2), based on the observation that those components showed less individual variability than the C1.

C1 localizer

Separate averages were calculated for responses to UP, LO, and FULL stimuli. Single electrodes with maximal C1 amplitude were identified for each participant. Values from these individually selected electrodes were then used for statistical analyses of the main-task data. In comparing C1 topographies obtained here with those observed in the main task, small deviations were observed in some subjects. However, the noise introduced into C1 measurements at this point is balanced by the use of independent measures for electrode localization and component quantification.

In an alternative analysis, we pooled data from 12 parieto-occipital electrodes across subjects to capture the C1. Separate but overlapping pools were used for UP and LO stimuli. Statistical results were equivalent for the single-electrode and electrode-

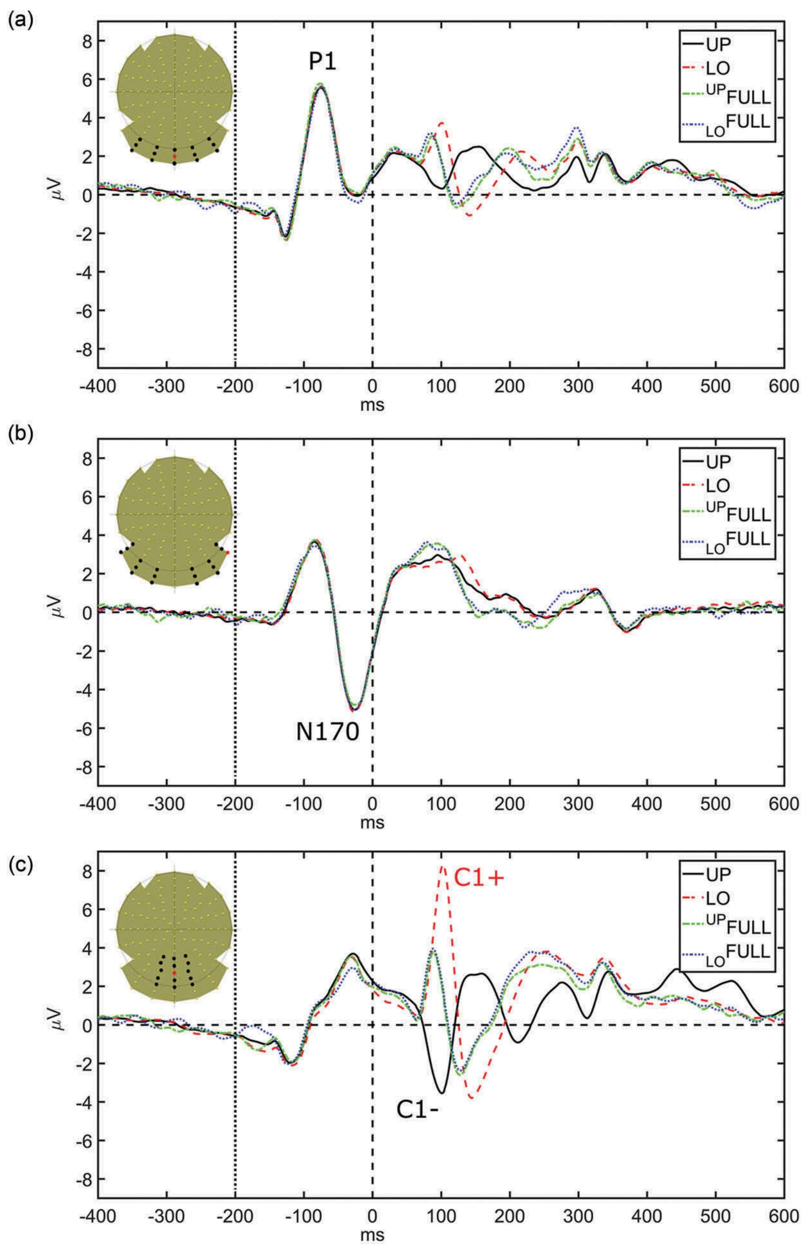

Figure 2. Grand-average ERPs show P1 (a) and N170 (b) components elicited by presentation of faces (dotted line at −200 ms). Subsequent presentation of peripheral lines (dashed line at 0 ms) elicited a C1 component (c), with the expected polarity reversal for UP vs. LO stimuli. Full-field stimulation elicited a positive followed by a negative deflection in the same interval, independent of whether stimulation was expected in the upper or lower visual field. Electrodes highlighted in insets were used to measure component peak amplitudes and latencies. Waveshapes are taken from electrodes highlighted in red.

pool approaches. For the sake of simplicity, we report single-electrode results. Electrode POz was centrally included in both LO and UP electrode pools, which is why we use it for display purposes.

Face localizer

Averages were calculated for happy and fearful faces separately, as well as for both emotions combined. Peak amplitudes and latencies of the face-selective N170 (Hinojosa, Mercado, & Carretié, 2015) were measured in each participant and compared between emotions.

Statistics

Peak amplitudes and latencies were compared between conditions using paired-samples *t*-tests or repeated-measures ANOVAs. In the latter case, Greenhouse–Geisser correction of degrees of freedom was applied whenever the assumption of sphericity was violated, as indicated by Mauchly's test. For better readability, we report original degrees of freedom.

Source localization

As detailed later, we also ran analyses based on awareness as a *post hoc* grouping factor. Given their exploratory nature, we used running *t*-tests to compare ERPs between groups at each time-point over the 500-ms interval following face onset (i.e., covering 200 ms before and 300 ms after lines onset). Differences were deemed significant if $p < 0.05$ for at least 10 consecutive time frames (≈ 20 ms) at five or more neighboring electrodes. Analyses were run in Cartool (version 3.55, 2014, Functional Brain Mapping Lab, University of Geneva, Switzerland; Brunet, Murray, & Michel, 2011). For intervals identified as significant, we then conducted distributed source localization using the LORETA algorithm (Pascual-Marqui, Michel, & Lehmann, 1994), as implemented in the LORETA-KEY software (version 2015-12-22, KEY Insitute for Brain-Mind Research, University of Zurich, Switzerland). The transformation matrix for inverse solutions was based on the MNI152 brain template and assumed a signal-to-noise ratio of 10. Individual ERPs were transferred to inverse space using the same matrix, and comparisons between and within groups were calculated using statistical nonparametric mapping based on 1000 randomizations. Data for both sample-wise *t*-tests and source localization were normalized by individual global field power, to account for interindividual differences in ERP amplitudes.

Results

Behavioral data

Main task

All 19 participants reached high levels of accuracy when asked to indicate the emotion of the previously presented face (percentage of correct trials (mean ± SE): 95.74 ± 0.78). Reaction times (RTs) for correct responses did not significantly differ between left and right buttons (1591 ± 39 vs.1563 ± 31 ms, $t(18) = 1.28$, $p = 0.217$), or between fearful and happy faces (1592 ± 34 vs. 1563 ± 36 ms, $t(18) = 1.357$, $p = 0.191$).

Face localizer

Results showed high levels of accuracy for all subjects for the emotion-detection task (percentage of correct trials: 92.11 ± 3.02). RTs did not significantly differ between right and left responses (1766 ± 41 vs. 1747 ± 51 ms, $t(18) = 0.396$, $p = 0.697$). However, there was a significant difference between emotions, with faster responses to happy than to fearful faces (1701 ± 47 ms vs.1812 ± 41, $t(18) = 2.602$, $p = 0.018$). Note that the C1 localizer was conducted under passive viewing conditions (i.e., no behavioral responses were collected).

Dot-probe task

One subject had to be excluded from analysis in this task due to a misunderstanding of task instructions. For the remaining 18 subjects, data were divided into congruent and incongruent trials. Congruent trials were defined as those in which the position of the dot matched the position of peripheral lines expected in the main task, based on the learned association between emotion and visual field location. We expected that this association would lead to better performance and shorter RTs for congruent trials compared to incongruent trials.

Dependent *t*-tests were performed to compare the two conditions, combining UP and LO trials. Results showed no difference between RTs for congruent and incongruent trials (356 ± 8 vs. 353 ± 8 ms, $t(17) = 0.775$, $p = 0.449$). Concerning accuracy of performance, there was no difference between conditions either (96.89 ± 0.80 vs. 96 ± 0.79, $t(17) = 1.215$, $p = 0.241$).

Assuming the association between the emotion of the face and a stimulus at a specific position is learned gradually over the course of the experiment, we then analyzed data from the two dot-probe blocks separately, with block number as an additional factor (the first dot-probe block was presented after the first half of main-task blocks, the second on at the end of the experiment, see Methods section.) We calculated a 2 × 2 repeated-measures ANOVA with congruency and block number as within-subject factors, both for RT and for accuracy. Results showed a significant effect of block number on RTs, indicating that subjects responded faster during the second block of the dot-probe task (362 ± 9 vs. 347 ± 8 ms, $F(17,1) = 12.931$, $p = 0.002$). As expected from the previous analyses, there was no main effect of congruency on RTs ($F(1, 17) = 0.648$, $p = 0.432$), and the interaction between block number and congruency also remained non-significant ($F(1,17) = 1.025$, $p = 0.325$). Analysis of accuracy data did not show any significant main or interaction effects (all *ps* > 0.222).

Awareness questionnaire

After the experiment, subjects were systematically questioned as to whether they were aware of the association between emotional expressions and the locations of subsequent peripheral stimuli. The questionnaire included a series of increasingly specific questions concerning this association. Participants were classified as aware if they could clearly and correctly verbalize the emotion–location association. Nine out of 19 participants noticed the association, while the other 10 participants did not. There were no significant differences between these two groups in terms of age, gender, or assignment to conditions of face–location association (all *ps* > 0.57). Additional analyses were conducted to test for potential differences on this *post hoc* factor (see later sections).

EEG data

Face localizer

Grand-averaged data for centrally presented faces showed the expected N170 for both happy (peak latency 170 ms after face onset) and fearful faces (peak latency 172 ms). Responses to happy and fearful faces were virtually equivalent. This was confirmed by an analysis of peak amplitudes detected in the time-window between 150 and 190 ms after face onset. The analysis was based on bilateral, temporo-occipital electrodes (as shown in Figure 2). A repeated-measures ANOVA with hemisphere (left vs. right) and emotion (fearful vs. happy) as within-subject factors showed a significant main effect of hemisphere, with higher N170 amplitudes on the right (left: −3.76 ± 0.47 µV; right: −5.26 ± 0.79 µV; $F(1, 18) = 4.792$, $p = 0.042$), in accordance with the known right-hemisphere advantage for face processing (Gschwind, Pourtois, Schwartz, Ville, & Vuilleumier, 2012). On the other hand, there was no significant effect of emotion on N170 amplitudes (fearful: −4.54 ± 0.55 µV; happy: −4.48 ± 0.57 µV; $F(1, 18) = 0.107$, $p = 0.747$), and the interaction between the two factors was also nonsignificant ($F(1, 18) = 2.246$, $p = 0.151$).

C1 localizer

Grand-averaged data for peripherally presented lines during blocks without foveally presented faces showed the expected C1 for both UP and LO stimuli, including a polarity inversion as a function of visual field location (Jeffreys & Axford, 1972). Peaks of the grand-averaged data were detected with positive polarity for LO stimuli (maximum +5.02 µV at 88 ms, electrode A21, corresponding to electrode POz in the International 10–20 System), and with negative polarity for UP stimuli (maximum −4.88 µV at 90 ms, also at electrode A21/POz). Grand-averaged data for FULL stimuli showed a wavelike pattern, with an initial negative peak (maximum −1.87 µV at 64 ms, POz) followed by a positive peak (maximum +2.01 µV at 94 ms, electrode A16, left parieto-occipital). Based on these data, we selected a time-window from 60 to 120 ms following onset of peripheral lines for semiautomatic detection of C1 peak amplitudes and latencies, as detailed in the Methods section.

Main task

The successive presentation of central faces and peripheral line arrays at a constant stimulus-onset asynchrony (SOA) of 200 ms evoked a characteristic sequence of overlapping potentials (Figure 2). Both the P1 and N170 components elicited by the face stimuli remained clearly distinguishable. The following P300, related to both the intrinsic and task relevance of the face stimuli, was overlaid by a C1 deflection at approximately 300 ms after face onset (i.e., 100 ms after lines onset). All subsequent components thus reflect the overlay of the two ERPs and the combined processing of the different stimuli.

Our main aim was to investigate whether learning the association between centrally presented emotions and subsequent peripheral stimuli would alter early visual cortex responses to unpredicted events in the periphery. While the grand-averages for ^{UP}FULL and $_{LO}$FULL conditions shown in Figure 2(c) did not indicate any obvious differences between conditions, this could be linked to the fact that C1 deflections of opposite polarity were overlaid on the P300 component elicited by the face stimuli. To address this possibility, we subtracted individual ERPs calculated from the face-localizer data from the same individual's main-task ERPs (see Methods section).

Following this subtraction procedure, visual inspection of both individual ERPs and grand-averages showed satisfactory removal of ERP components elicited by face stimuli preceding peripheral line arrays (Figure 3). Importantly, a clear C1 was detected following UP and LO stimuli, both in individual and in grand-averaged data. However,

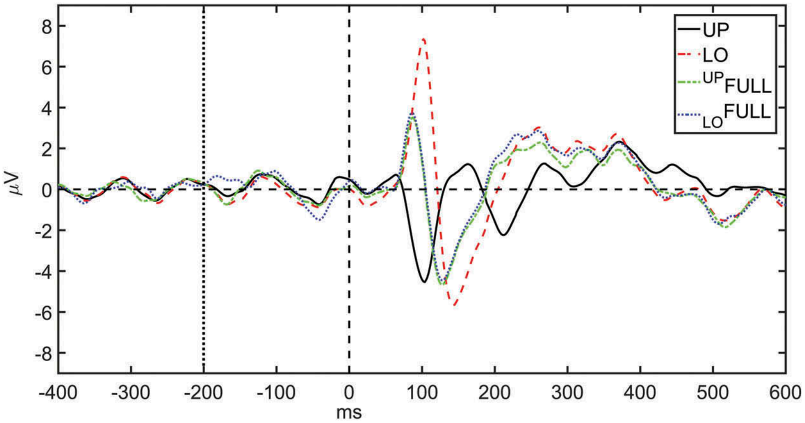

Figure 3. Grand-average C1 responses following subtraction of individual ERPs obtained from the face-localizer block. The plots for all conditions indicate large-scale removal of face-related ERPs during the period preceding lines onset at 0 ms. Cleaned C1 estimates appear similar to C1 responses overlaid onto the face-elicited P3 (cf. Figure 2(c); waveshapes are shown for the same electrode, corresponding to POz).

unilateral stimuli in the main task elicited later C1 responses than in the C1 localizer, as shown by analysis of individually detected maxima for both LO (C1 localizer: 83 ± 2 ms; main task: 95 ± 1; $t(18) = -6.708$, $p < 0.001$) and UP stimuli (C1 localizer: 89 ± 2 ms; main task: 102 ± 2; $t(18) = -6.039$, $p < 0.001$). Furthermore, comparison of C1 peak amplitudes indicated stronger early visual cortex responses in the main task than in the C1 localizer for LO stimuli (C1 localizer: 7.73 ± 0.63 µV; main task: 8.72 ± 0.65 µV; $t(18) = -2.202$, $p = 0.041$), but weaker responses for UP stimuli (C1 localizer: −6.78 ± 0.66 µV; main task: −5.76 ± 0.70 µV; $t(18) = -2.575$, $p = 0.019$). This discrepancy may be linked to incomplete removal of face-related activity by our subtraction procedure, which could have exaggerated the positive C1 following LO stimuli and diminished the negative C1 following UP stimuli. On the other hand, nonlinearities surviving our subtraction procedure could also be due to expectancy effects induced in the main task that are absent in the localizer data, including differences in task contexts between localizer (passive viewing) and main-task (short-term memory task).

We then isolated responses to expected and unexpected parts of FULL stimuli via a second set of subtractions (see Methods section). The resulting difference ERPs were taken to reflect predictions and prediction errors, respectively, and we compared them to the responses to expected half-field stimuli. Given the known asymmetries between upper and the lower visual fields (Pourtois et al., 2008; Rauss et al., 2009; Skrandies, 1987), we conducted separate analyses for lower and upper visual fields.

For the lower visual field, there was no significant effect of prediction on C1 amplitudes (LO: 8.72 ± 0.65 µV; P_{LO}: 8.61 ± 0.84 µV; PE_{LO}: 8.36 ± 0.81 µV; $F(2, 36) = 0.202$, $p = 0.701$). The same analyses computed for the upper visual field showed a significant effect of prediction on C1 amplitudes (UP: −5.76 ± 0.70 µV; P^{UP}: −7.37 ± 0.79 µV; PE^{UP}: −7.27 ± 0.89 µV; $F(2, 36) = 5.457$, $p = 0.020$; see Figure 4). Post hoc t tests showed significant differences only between UP and both P^{UP} ($t(18) = 2.682$, $p = 0.015$) and PE^{UP} ($t(18) = 2.281$, $p = 0.035$) but not between the two bilateral conditions ($t(18) = -0.303$, $p = 0.766$).

Taken together, these results do not provide evidence for retinotopically specific effects of a mismatch between prediction and actual visual stimulation in our protocol. The finding of enhanced C1 amplitudes following bilateral stimulation may indicate a more global surprise signal to the rare FULL stimuli, potentially reflecting a very early mismatch response. Alternatively, interindividual differences in attentional control or emotional reactivity could have obscured the expected C1 differences. However, face-evoked components did not correlate with STAI scores (P1, $p = 0.60$; N170, $p = 0.57$), and neither did we observe any relationship between distractibility and C1 amplitudes (ACS, all $ps > 0.08$; CFQ, all $ps > 0.23$; uncorrected for multiple comparisons). In contrast, consideration of the awareness

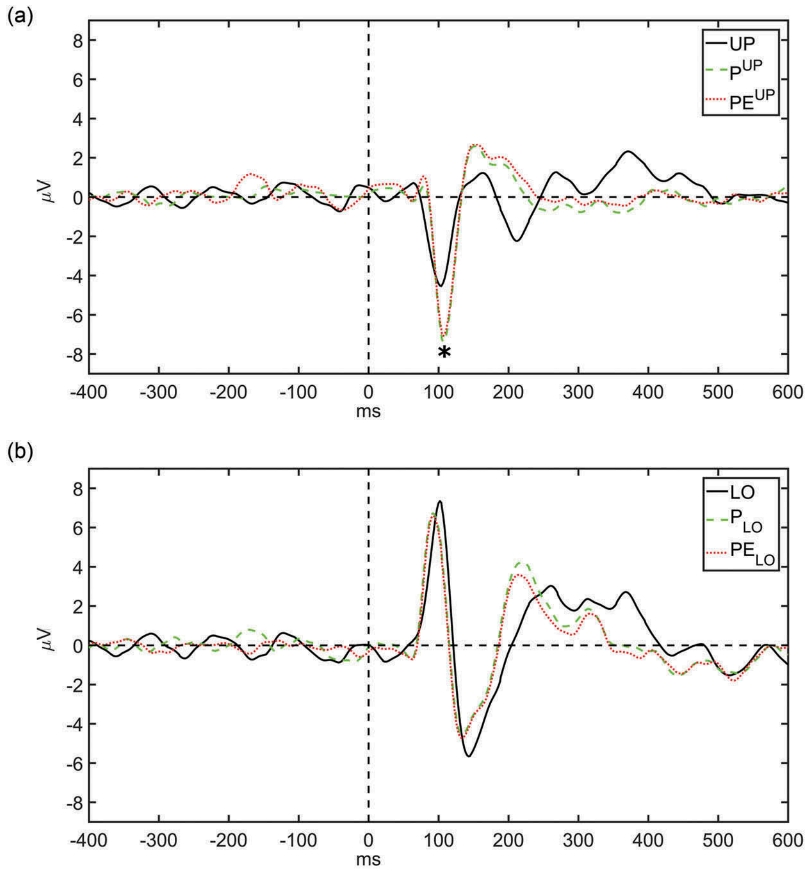

Figure 4. Grand-average C1 responses compared to difference ERPs reflecting predicted and unpredicted stimuli at the same location. (a) Upper visual field effects. P^{UP} shows C1 responses to ^{UP}FULL stimuli after subtracting ERPs to LO stimuli obtained in the C1 localizer block, thus reflecting the response to the predictable part of FULL stimuli. Conversely, PE^{UP} shows ^{UP}FULL responses after subtraction of UP responses from the C1 localizer, thus reflecting the unpredicted part of FULL stimuli. Both P^{UP} and PE^{UP} C1 responses were significantly more negative than those elicited by expected UP stimuli ($p = 0.020$). However, they did not differ from each other, thus providing no evidence for retinotopically specific mismatch responses during the C1 interval. (b) Corresponding data for lower visual field conditions do not indicate any significant differences between LO, P_{LO}, or PE_{LO} at the C1 level. Data in both panels are shown for electrode POz.

questionnaire showed that ERP results were indeed affected by whether subjects noticed the relation between emotional faces and peripheral lines.

Effects of awareness

During debriefing, subjects were asked a series of increasingly specific questions concerning their awareness of the association between emotional facial expressions and spatial locations of subsequent peripheral stimuli. Roughly half of our sample (9/19) spontaneously became aware of emotion–location associations, with unequivocal classification in all cases. Specifically, all aware subjects immediately reported their respective associations when asked whether they 'noticed anything particular during the experiment,' whereas unaware subjects could not report these associations even when prompted whether 'they noticed a link between the emotion of the faces and the location of the peripheral lines.'

In order to assess whether spontaneous awareness of emotion–location associations affected VEPs, we performed comparisons between groups of aware and unaware subjects. We emphasize that these analyses are *post hoc* in nature and that their results therefore need to be interpreted with caution. Nevertheless, we believe they are relevant for understanding the present data and highlight an important avenue for future research.

At the behavioral level, no significant differences were observed between aware and unaware subjects, either for control questionnaires (all $ps > 0.740$), main-task RTs and accuracy data (all $ps < 0.279$), or dot-probe RTs ($p = 0.214$). A marginally significant difference was seen for dot-probe accuracy data, with slightly better performance in aware subjects (unaware: 95.22 ± 0.94; aware 97.67 ± 0.97, $F(1, 16) = 3.413$, $p = 0.083$).

At the electrophysiological level, we first examined whether groups of aware and unaware subjects differed in their ERP responses to unexpected FULL stimuli. To do so, we used exploratory, sample-wise t-tests which were conducted separately for ^{UP}FULL and $_{LO}$FULL conditions. Whenever such differences were observed, we pinpointed their neural sources using LORETA distributed source localization (Pascual-Marqui et al., 1994).

Data from the ^{UP}FULL condition indicated significantly higher activity in unaware subjects during the P1 interval (110–150 ms after face onset; differences were deemed significant if $p < 0.05$ for ≥20 ms at five or more adjacent electrodes, see Methods section). This effect was localized to visual areas, with a maximum in the left lingual gyrus ($p < 0.01$; Brodmann area [BA] 19; Montreal Neurological Institute (MNI) coordinates −10, −55, −5; Figure 5(a)) extending back to BA 18 and forward to the parahippocampal gyrus. During the same interval, a small source showing more pronounced activity in aware subjects was seen in right medial frontal gyrus ($p < 0.5$; BA 10; MNI 5, 65, 20; data not shown).

A second interval of significant differences at the scalp was seen between 65 and 90 ms after lines onset (i.e., 265–290 ms after face onset), with higher activity in aware subjects at parieto-occipital leads. Source localization indicated a significant increase of activity in aware subjects in the left precuneus ($p < 0.01$; BA 7; MNI −5, −50, 50; Figure 5(b)), extending into the paracentral lobule and cingulate gyrus. Over the same interval, unaware subjects showed higher activity in right middle occipital gyrus, albeit at a lower level of significance ($p < 0.05$; BA 19; MNI 40, −90, 5; data not shown), extending over BA 18 and into the cuneus and BA 17.

In the $_{LO}$FULL condition, unaware subjects also showed higher activity during the P1 interval (100–145 ms after face onset). Source localization again indicated significantly higher activity in unaware subjects in left lingual gyrus ($p < 0.01$; BA 19; MNI −10, −60, −5; Figure 5(c)), extending into posterior cingulate and parahippocampal cortex at lower thresholds. Concurrently, higher activity in aware subjects was seen in left medial frontal gyrus ($p < 0.05$; BA 10; MNI −5, 65, 20; partly visible in Figure 5(c)).[1]

In order to determine whether these group differences were present even before any learning of emotion–location associations took place, we went back to the face localizer data, which were acquired during the first block of the experiment. Because we did not find differences between fearful and happy faces in previous analyses, the two conditions were combined. Running t-tests indicated significant differences immediately after face onset (10–30 ms), which are likely due to noise fluctuations in the absence of stimulus-evoked cortical activity during this interval. More interestingly, higher activity for unaware subjects was seen at occipital leads between 100 and 130 ms after face onset, concurrently with higher activity at left temporal electrodes in aware subjects. Source localization indicated widespread differences even at a threshold of $p < 0.01$, predominantly in the left hemisphere, with a maximum in the precuneus (BA 31; MNI −15, −60, 25), extending into both early visual areas (BAs 18, 19) as well as posterior cingulate cortex, lingual gyrus, and parahippocampal cortex.

Taken together, these results show that the presentation of emotional faces elicited more widespread activation in unaware subjects, predominantly in early visual areas, but also further along the ventral stream. The fact that these differences were present before any associative learning had taken place hints at individual differences underlying the spontaneous emergence of conscious awareness of even simple (albeit task-irrelevant) associations. This raises the question whether such differences in face-processing and awareness could have overlaid putative mismatch signals in early visual cortex.

To address this question, we reinvestigated the C1 data from the main task blocks. We first ran separate analyses for aware and unaware subjects based on the prediction- and prediction-error-subtractions detailed earlier. Results showed the same numerical differences between the UP condition on the one hand and P^{UP} and PE^{UP} conditions on the other in

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[1] In addition, aware subjects showed higher activity between 110–180 ms after lines onset (i.e., 310–380 ms after face onset) at right temporoparietal electrodes; and between 220 and 280 ms after lines onset (420–480 ms after face onset), unaware subjects displayed higher activity at occipital and bilateral parieto-temporal scalp sites, whereas activity at fronto-central electrodes was more pronounced in aware subjects. In both cases, source analysis did not uncover significant group differences, probably due to a combination of small group sizes and the fact that we used template-based source reconstructions that do not account for interindividual differences in brain anatomy.

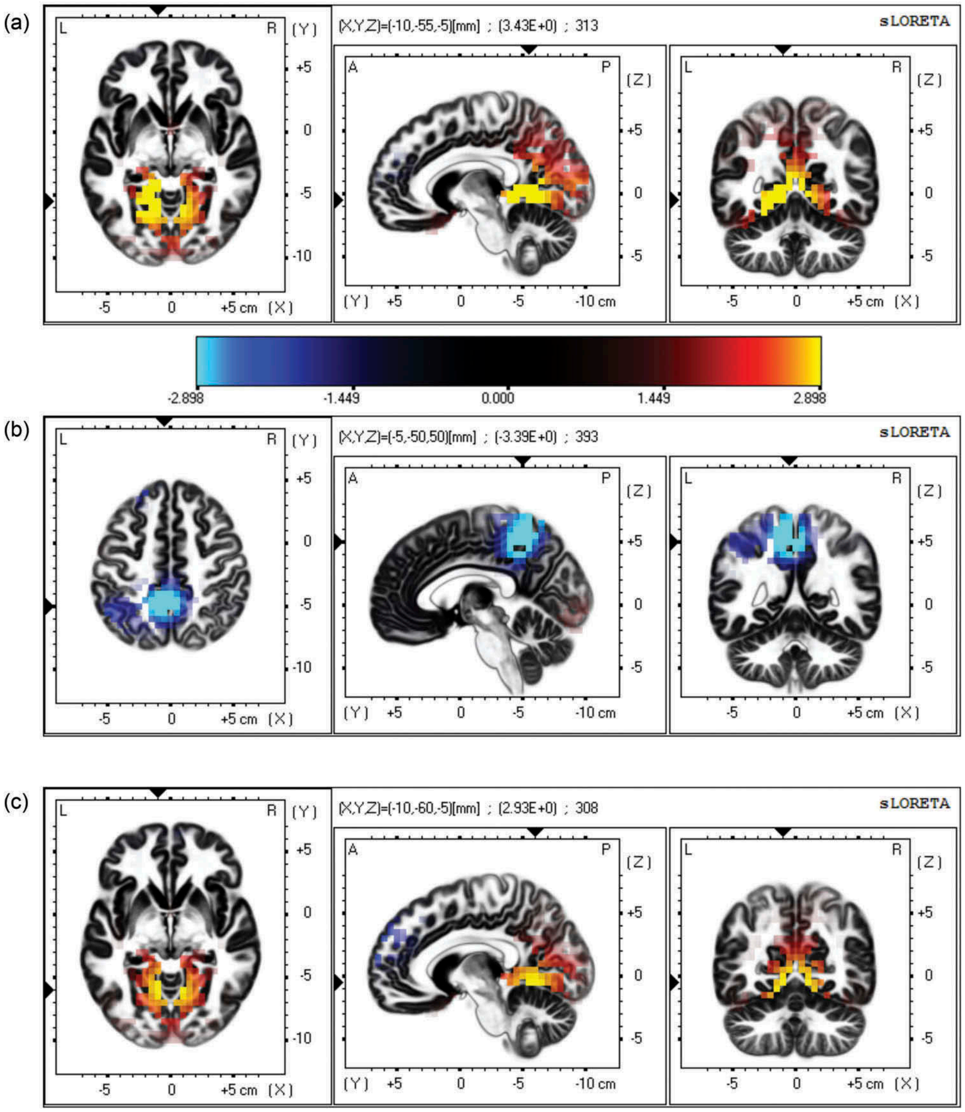

Figure 5. Exploratory comparisons between groups of manipulation-aware and—unaware subjects. Periods of significant activity differences were determined via sample-wise *t*-tests ($p < 0.05$ for at least 20 ms at five or more adjacent electrodes) and subsequently analyzed with distributed source localization (sLORETA). Images show the results of unpaired *t*-tests with unaware subjects as the reference group (i.e., positive values reflect higher activity in unaware subjects). All images are scaled to *t*-values of 2.898, corresponding to $p < 0.01$ with $df = 17$. (a) Results for condition ^{UP}FULL show that unaware subjects exhibit higher activity in ventral visual cortex during the P1 interval (110–150 ms following face onset). (b) Conversely, aware subjects show increased neural responses in the precuneus during the early C1-interval (65–90 ms following lines onset. (c) In the $_{LO}$FULL condition, unaware subjects again exhibit higher activity in ventral visual cortex during the P1 interval (100–145 ms following face onset); higher medial frontal activity in aware subjects during the same interval is partly visible.

both groups. This difference was significant only in unaware subjects ($F(2, 8) = 4.84$, $p = 0.039$), probably due to lack of power in the even smaller group of aware subjects. The small resulting group sizes may be particularly problematic in the context of peak-amplitude measures computed on difference waves, as employed here. We therefore implemented the same analysis in inverse space. This allows us to statistically compare ^{UP}FULL and $_{LO}$FULL conditions without first subtracting expected or unexpected stimulus elements at the scalp level. Given our original hypothesis, we specifically focused on the early phase of the C1 (60-90 ms; Foxe & Simpson, 2002) and its subsequent transition into the P1 (90–120 ms). In order to obtain a clean estimate of responses to peripheral lines, we subtracted face-evoked activity in inverse space: inverse solutions were calculated for ERPs from the face localizer

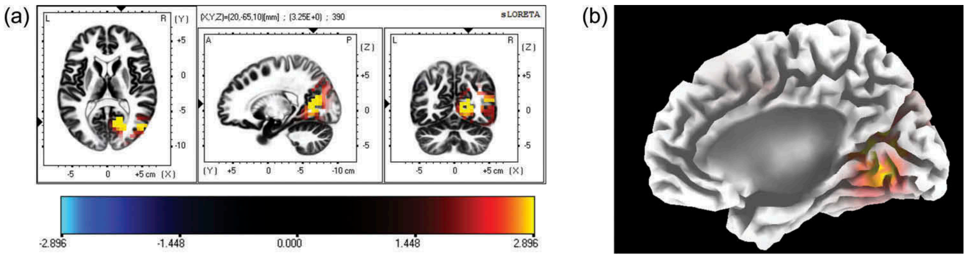

Figure 6. Comparison of inverse solutions for prediction-error conditions (aware subjects only).
(a) Maximal differences were observed in right posterior cingulate, extending into early visual areas, as well as right middle temporal gyrus (not shown). Warm colors reflect higher activity in the $_{\text{LO}}$FULL condition, where stimuli where expected in the lower visual field, but both upper and lower visual field were stimulated. (b) The same data rendered onto the medial surface of the right hemisphere. Localization of the effect is in accordance with the notion of enhanced prediction-error signals in ventral visual areas due to unexpected stimulation of the upper visual field. However, corresponding effects in the opposite direction in dorsal early visual cortex were not detected.

block and subtracted from inverse solutions for main-task ERPs before comparing the latter between $^{\text{UP}}$FULL and $_{\text{LO}}$FULL conditions within groups.

In unaware subjects, these analyses indicated higher activity in the $_{\text{LO}}$FULL condition during the early C1 interval in a small region in superior frontal gyrus, on the border between BA 8 and BA 9. No significant differences were seen during the subsequent C1-P1 transition interval.

In aware subjects, two regions exhibited higher activity in the $_{\text{LO}}$FULL condition during the early C1 interval: the first was centered on right posterior cingulate ($p < 0.01$; BA 30; MNI 20, −65, 10; Figure 6 (a)), extending into right cuneus and lingual gyrus (BAs 18, 19), whereas the second was located in right middle temporal gyrus ($p < 0.01$; BA 30; 55, −70, 15). The latter difference persisted into the 90–120-ms interval at a lower threshold ($p < 0.05$), accompanied by differences in precentral (BA 6) and cingulate gyri (BA 24; both $p < 0.05$).

In sum, within-group analyses suggest that modulations in early visual processing can occur for the same physical stimuli if parts of these stimuli are unexpected due to associative learning. However, these modulations were only observed in participants who were aware of the association between foveally presented emotions and peripherally presented lines, a result requiring confirmation and replication with larger samples and active manipulations of awareness.

Discussion

In the present study, participants were exposed to systematic associations between foveally presented emotional faces and peripherally presented line arrays. We hypothesized that these associations would be implicitly learned, and that this learning would lead to retinotopically specific mismatch signals at the level of the C1 component of the VEP when associations are subsequently violated on infrequent test trials. Results over our full sample of 19 participants did not support the idea of such a very early error signal. This was mirrored in the behavioral data, which did not indicate significant transfer of associations to a different task context (i.e., dot-probe task), either in terms of shortened RTs or in terms of improved accuracy.

The absence of behavioral learning effects suggests that stimulus associations were only weakly encoded. This could be due to the fact that peripheral line arrays were never task-relevant, or to the limited number of association trials which may not have been sufficient to enable robust learning in all participants. A third possibility is that extraction of emotional information from foveally presented faces was hindered by the subsequent presentation of peripheral line arrays after a brief interval of only 200 ms. The literature suggests that emotional information can be rapidly extracted from face images (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Szczepanowski & Pessoa, 2007), but the extent of emotional processing at the level of the N170 component remains subject to debate (Hinojosa et al., 2015). In this context, it is possible that our stimulus timing served to highlight individual differences in face processing and how they affect associative learning.

Several methodological challenges may also have affected our ability to detect potent PE signals in early visual processing across our full sample using scalp EEG. Thus, we chose a short, fixed interval between foveal and peripheral stimuli, in order to enable spatiotemporally precise predictions. Variable interstimulus or response-to-stimulus intervals have been shown to impede learning, for example in serial RT tasks (Stadler, 1995; Willingham, Greenberg, & Thomas, 1997). However, our use of a fixed SOA required subsequent subtraction of separately recorded face-ERPs from the responses elicited by the combined presentation of faces and peripheral lines. Incomplete removal of face-evoked responses may have reduced the sensitivity of our statistical comparisons. The averaging inherent in the ERP method does not allow us to distinguish whether such incomplete removal reflects methodological limitations, or whether it is related to the gradual learning of stimulus associations. It remains to be tested whether the use of a jittered SOA would improve sensitivity in our protocol by rendering ERP subtraction obsolete, despite making predictions less precise in the temporal domain.

We also opted to present the same physical stimuli in order to violate predictions of upper vs. lower visual field stimulation. This was done to enable direct comparisons between prediction and predition-error conditions. Simply switching the test stimulus from the predicted to the unpredicted half-field would have made this comparison impossible, as absolute amplitudes to upper and lower visual field stimulation can vary considerably within subjects (Kelly et al., 2008). However, this choice entailed the use of a second subtraction procedure, in order to remove responses to predicted or unpredicted parts of the full-field stimuli. Future studies could improve on the present procedure by including a baseline condition where, for example, a third emotion is predominantly associated with full-field stimuli, thus capturing potential adaptation effects to the latter.

In summary, across our sample of 19 participants, associations of emotional faces with peripheral spatial locations did not induce the expected PE signals at the level of early visual ERP components. Behavioral data and methodological considerations suggest that this may be due to the fact that robust associative learning was not achieved across the full sample.

Based on a clear and equal split of participants into those who did and those who did not consciously perceive emotion–location associations, we conducted additional, *post hoc* analyses comparing these groups. Behaviorally, aware subjects performed marginally better than unaware subjects in the dot-probe task, suggesting some degree of associative learning with subsequent transfer to a different task. At the neurophysiological level, we found that unaware subjects recruited more neural resources to process emotional faces at fixation. This effect was present as early as the extrastriate P1 component, starting around 100 ms after face onset. Importantly, this was independent of task-context and learning, which suggests that pre-existing interindividual differences in extrastriate face processing may have rendered participants more or less likely to detect emotion–location associations.

Pronounced interindividual differences have been reported in response to masked human faces (Pessoa, Japee, Sturman, & Ungerleider, 2006; Zhang, Wang, Luo, & Luo, 2012), as well as in basic visual search tasks (Papera & Richards, 2016), or attentional blink protocols (Martens, Munneke, Smid, & Johnson, 2006). Such differences are usually explained in terms of interindividual variance in attentional resources. However, P1 amplitudes in our sample did not correlate with questionnaire measures of attentional parameters, either in the main task or in the face localizer data (Attentional Control Scale, all *ps* > 0.47; Cognitive Failures Questionnaire, all *ps* > 0.44). One possibility is that the emotional content of facial expressions specifically engaged more processing resources in unaware subjects (Pourtois, Schettino, & Vuilleumier, 2013), leaving them less likely to notice the association with immediately subsequent peripheral stimuli. However, P1 amplitudes were not correlated with emotional control parameters either (STAI, $r = -0.13$, $p = 0.300$). We also note that our stimuli (Ekman & Friesen, 1976) are only weakly emotional as compared to other stimulus sets (e.g. the International Affective Picture System, IAPS; Lang, Bradley, & Cuthbert, 1997). Additional studies using more detailed profiling of attentional and emotional parameters will be required in order to clarify the origins of differences between our manipulation-aware and -unaware participants.

Additional exploratory analyses were conducted within groups, to examine whether our original hypothesis might apply selectively to one of our *post hoc* groups. Consequently, these analyses focused on the C1 interval and compared activity patterns between the two conditions with unexpected peripheral stimulation (i.e., ^{UP}FULL and $_{LO}$FULL). In unaware subjects, we observed a small difference in left superior frontal gyrus. In the present context, this effect may be due to incomplete removal of face-evoked activity during subtraction in inverse space. However, differences in task contexts between face-localizer and main-task blocks cannot explain why activity at this prefrontal location should differ between the same physical stimuli as a function of stimulus associations which were not consciously noticed by these subjects. One possibility is that unaware subjects engaged additional, higher-order resources to a greater extent or over a longer period of time in order to construct a valid model of the main task. The visual system is highly adept at extracting statistical regularities from the environment, even in the absence of conscious awareness (Turk-Browne, Jungé, & Scholl, 2005). According to predictive-coding models, violations of such regularities should subsequently lead to a cascade of PE signals along sensory and higher cognitive brain structures (Clark, 2013; Friston & Frith, 2015; Rauss & Pourtois, 2013). In the absence of a valid internal model of the main task, PE signals in response to full-field stimuli would need to be resolved at higher levels of processing in unaware than aware subjects. Importantly, it has been shown that stimulus-evoked prefrontal cortex activity can precede the C1 peak (Foxe & Simpson, 2002; Hupé et al., 2001).

Results in aware subjects indicated that the same arrays of peripheral line elements elicited different activity patterns during the C1-P1 interval, starting 60 ms after lines onset, depending on which part of the stimulus was unexpected. However, we acknowledge that a stringent test of this effect as a group × expectation interaction was not possible due to the fact that our sample size was not optimized for the additional group factor. The precise nature of the differences in early visual processing observed in aware subjects is difficult to assess within the limits of template-based source localization methods as employed here. Nevertheless, the effect's direction and approximate location on the medial surface ventral to the calcarine sulcus correspond with our hypothesis of a retinotopic effect: source activity was greater in the $_{LO}$FULL condition, for which we predicted error signals related to the unexpected upper part of the stimulus, as represented in the ventral calcarine sulcus. However, the same hypothesis also predicts higher activity in the dorsal calcarine following ^{UP}FULL stimuli, which we did not observe. Given the large variability in visual cortex anatomy (Dougherty et al., 2003; Kelly et al., 2008), as well as known anisotropies between the upper and lower visual fields (Previc, 1990; Skrandies, 1987), follow-up studies will have to rely on larger samples and/or individually tailored inverse solutions (J. Ales, Carney, & Klein, 2010) to address this inconsistency.

Early prediction and prediction-error signals have been reported in mouse V1 (Gavornik & Bear, 2014; Shuler & Bear, 2006), and predictive processes operate in human V1 (Kok, Bains, Van Mourik, Norris, & De Lange, 2016; Kok et al., 2012; Muckli, Kohler, Kriegeskorte, & Singer, 2005; Smith & Muckli, 2010). Our findings suggest that the latter can occur during early stages of visual processing, but only if subjects are consciously aware that certain stimuli are predictable. On the other hand, due to small effective group sizes, it could also be that this apparent dichotomy actually reflects a continuum of awareness and early predictive coding. Our use of an easy 1-back task at fixation combined with the instruction to ignore peripheral stimuli may have served to highlight individual differences in terms of pattern-searching under relatively undemanding conditions. A more demanding fixation-task and/or a secondary task to be performed on the peripheral stimuli could be used to reinforce associative learning while at the same time ensuring it remains implicit. Indeed, such an adapted protocol might also enhance the contribution of predictive processes such as expectation suppression (John-Saaltink, Utzerath, Kok, Lau, & De Lange, 2015). An unequivocal test of the hypothesis suggested by our exploratory analyses will require direct experimental manipulations of conscious awareness.

Conclusion

The present study does not provide evidence for early retinotopic mismatch signals at the C1 level across a sample of 19 healthy participants. Behavioral and EEG data suggest that this null finding may be linked to a lack of learning of stimulus associations across subjects. Several task parameters may have conspired to reduce associative learning. These elements need to be addressed in future studies in order to test whether early, retinotopic PE signals may occur when stimulus associations are more robustly established and maintained.

Exploratory analyses additionally uncovered spontaneous awareness as a subject-specific parameter with potentially strong effects in the present task: they provide preliminary evidence for the notion that human early visual cortex activity can encode PE signals if subjects are consciously aware of predictable stimulus elements. Between-group comparisons of ERP inverse solutions suggest that additional resources recruited to process emotional faces in extrastriate areas kept unaware participants from noticing emotion–location associations; whereas within-group analyses indicate differences in the representation of the same peripheral stimuli as a function of whether they are expected or not. This effect was present as early as 60 ms after stimulus onset, and was selectively seen in aware subjects. Its timing, location, and direction provide initial support for our hypothesis of retinotopically specific mismatch signals in early visual processing, but this effect will have to be replicated in larger samples using more advanced methods of source localization and direct manipulations of conscious awareness.

Disclosure statement

No potential conflict of interest was reported by the authors.

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