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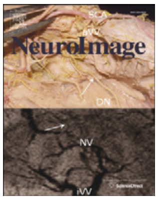

Multiple synergistic effects of emotion and memory on proactive processes leading to scene recognition

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ABSTRACT

Visual scene recognition is a proactive process through which contextual cues and top-down expectations facilitate the extraction of invariant features. Whether the emotional content of the scenes exerts a reliable influence on these processes or not, however, remains an open question. Here, topographic ERP mapping analysis and a distributed source localization method were used to characterize the electrophysiological correlates of proactive processes leading to scene recognition, as well as the potential modulation of these processes by memory and emotion. On each trial, the content of a complex neutral or emotional scene was progressively revealed, and participants were asked to decide whether this scene had previously been encountered or not (delayed match-to-sample task). Behavioral results showed earlier recognition for old compared to new scenes, as well as delayed recognition for emotional vs. neutral scenes. Electrophysiological results revealed that, ~400 ms following stimulus onset, activity in ventral object-selective regions increased linearly as a function of accumulation of perceptual evidence prior to recognition of old scenes. The emotional content of the scenes had an early influence in these areas. By comparison, at the same latency, the processing of new scenes was mostly achieved by dorsal and medial frontal brain areas, including the anterior cingulate cortex and the insula. In the latter region, emotion biased recognition at later stages, likely corresponding to decision making processes. These findings suggest that emotion can operate at distinct and multiple levels during proactive processes leading to scene recognition, depending on the extent of prior encounter with these scenes.

Introduction

Visual scene recognition results from dynamic and reciprocal interactions between bottom-up sensory processing and top-down modulatory influences, including selective attention (Treisman and Kanwisher, 1998), contextual information (Oliva and Torralba, 2007), and prior expectations (Summerfield and Egner, 2009). Interestingly, it has been proposed that the differential sensory processing of low (LSF) and high (HSF) spatial frequency information could underlie reciprocal interaction effects between bottom-up sensory processing and top-down expectations (Bar, 2003, 2004, 2007). In this framework, the rapid extraction of LSF information via dedicated magnocellular pathways may serve to quickly generate coarse predictions regarding the most probable content of the visual scene. This process would later be assisted and refined by the extraction of HSF information.

Whether these dynamic perceptual processes are differentially engaged depending on the (perceived) emotional content of the scenes, however, has received little attention so far. Mounting evidence shows that emotion exerts strong biases on visual perception (Öhman et al., 2001; Pourtois et al., 2013; Todd et al., 2012; Vuilleumier, 2005), including at early stages of recognition (Damaraju et al., 2009; Halgren et al., 2000; Pourtois et al., 2004). Thus, emotion is no longer seen as a byproduct of perception but, instead, as a core determinant of it (Pourtois et al., 2013). Accordingly, proactive processes during scene recognition are unlikely to be immune to emotion, defined here as the acquired valence and arousal values of the stimulus (Barrett et al., 2007; Lang, 1995; Russell, 1980). More specifically, the speed and extent of iterative processes between bottom-up processing and top-down expectations during scene recognition are probably subject to variations depending on the rapidly extracted emotional meaning of the stimulus. Consistent with this assumption, we recently reported evidence for the modulation of scene recognition processes by emotion (Schettino et al., 2011). In this study, participants were presented with series of pictures whose content was progressively revealed by increasing, in up to six sequential steps, the amount of LSF and HSF information. This *progressive unfolding task* was used to mimic a "coarse-to-fine" decomposition of the retinal input, presumably fostering the online generation of guesses regarding the most likely identity of the stimulus (Bar, 2003; Bullier, 2001; Hegdé, 2008).

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Participants were asked to discriminate the content of the stimulus progressively revealed by performing an orthogonal animacy judgment task. Crucially, the scenes used in this experiment were neutral, pleasant, or unpleasant. Behavioral results showed a delayed recognition for emotional compared to neutral scenes. At the electrophysiological level, we found reliable ERP differences starting at approximately 280 ms after stimulus onset, depending on the amount of perceptual evidence accumulated. Estimated activity in the posterior cingulate cortex (PCC) and the parahippocampal gyrus (PHG) showed a response profile characterized by a linear and monotonic accumulation of perceptual evidence. Conversely, categorical recognition effects were evidenced in medial frontal regions, including the dorsal anterior cingulate cortex (dACC). However, none of these brain effects, albeit consistent with previous neuroimaging results (Carlson et al., 2006; James et al., 2000; Ploran et al., 2007, 2011), was found to be influenced by the emotional content of the scenes.

This lack of modulatory effect of emotion on these brain mechanisms was imputed to two main factors. First, it was hypothesized that the elected procedure did not effectively promote the generation of unambiguous predictions regarding the likely identity of the scenes progressively revealed, since participants were mainly presented with visually impoverished versions of pictures that they had never encountered before. Second, the use of an orthogonal animacy judgment task might have strongly reduced the salience of the emotional features of the scenes. Several studies showed that (early and automatic) affective stimulus processing is substantially reduced when concurrent, non-affective semantic stimulus dimensions become task-relevant (Everaert et al., 2011; Pessoa, 2008; Pessoa et al., 2002; Spruyt et al., 2007). To overcome these limitations, we devised a modified version of the progressive unfolding task (Schettino et al., 2012). In this latter study, to promote the generation and use of a restricted number of predictions regarding the identity of the scenes progressively revealed, we introduced a standard delayed match-to-sample manipulation (Courtney et al., 1997; Goldman-Rakic, 1990; Henson et al., 2005; Rugg et al., 1998). On each trial, participants were first asked to encode a complex colorful scene having either a neutral or emotional meaning. After a constant time interval, the content of either the same or a novel scene was progressively revealed (similarly to Schettino et al., 2011), and participants were asked to perform a delayed match-to-sample task. In addition, we occasionally asked participants to rate the emotional content of the scenes (besides the delayed match-to-sample task), thereby ensuring that the emotion features were directly attended throughout the whole experimental session. Behavioral results revealed earlier recognition for old compared to new scenes in all emotion conditions, providing evidence that participants used restricted (short-term) memory representations to perform the task. Notably, delayed recognition was observed for emotional relative to neutral scenes, replicating our previous behavioral results (Schettino et al., 2011).

The present paper reports the electrophysiological results of the aforementioned behavioral study (Schettino et al., 2012). Our main objective was to compare, using advanced EEG methods, the processing of previously encountered ("old") vs. "new" scenes, in order to evaluate whether any influence of emotion on brain mechanisms underlying scene recognition was depending on the (short-term) memory status of these complex visual stimuli. To verify that our short-term memory manipulation was effective, we analyzed a distinctive ERP signature of recollection processes, a late positive ERP waveform typically recorded from centro-parietal sites starting at approximately 500 ms post-stimulus onset (Curran and Cleary, 2003; Curran and Doyle, 2011; Rugg and Curran, 2007; Voss and Paller, 2006). Based on previous literature, we expected to observe more positive ERPs after correctly recognized old pictures compared to correctly classified new pictures, the so-called 'old/new effect' (Rugg and Curran, 2007; Voss and Paller, 2008; Wilding et al., 1995). Topographic analysis and complementary source localization methods were subsequently employed to investigate whether dissociable response profiles could be evidenced as a function of memory status and emotional valence of the scenes. Similarly to our previous study (Schettino et al., 2011), reliable topographical differences were expected to be observed in a time window following the low-level visual discrimination of the stimulus (i.e., after the N1 and P2 ERP components). In addition, we used a standard distributed source localization method to estimate the configuration of the neural generators of the main topographical maps identified by the preceding analysis. We assessed whether differential activation profiles in specific ventral brain areas as opposed to dorsal/medial frontal regions might be found, reflecting accumulation of evidence and decision-related processes, respectively.

Methods

Participants

Twenty-two undergraduate psychology students (all women, mean age 21 years, range 18–26) participated in the study, which was approved by the local Ethics Committee. All participants were native Dutch speaking, right-handed, had normal or corrected-to-normal vision, with no history of neurological or psychiatric disorders. The data of one participant could not be saved properly because of technical problems, whereas the EEG data of three other participants were discarded due to excessive artifacts and a low signal-to-noise ratio. Thus, the final sample consisted of 18 participants. All volunteers gave informed written consent prior to their participation, and were compensated 30 €.

Stimuli

The visual stimuli were selected from the International Affective Picture System (IAPS; Lang et al., 2008). Three-hundred and sixty pictures were pre-selected, equally divided into three emotion categories according to their pre-defined valence scores: *neutral*, *unpleasant*, and *pleasant* (see Table 1 in Schettino et al., 2012). Of note, these pictures were selected on the basis of mean valence and arousal ratings reported by female responders (Lang et al., 2008), because only women eventually participated in the experiment (see above). Similar to Schettino et al. (2011), we selected scenes that were neither highly pleasant (i.e., erotic situations) nor highly unpleasant (i.e., mutilations), because these categories were associated with specific emotion reactions in previous research (Schupp et al., 2006, 2007). We also included 16 additional neutral pictures that were only used during the practice session (not included in the subsequent statistical analyses). Furthermore, 36 supplementary neutral scenes were scrambled (i.e., each scene was divided into arbitrary grids of 255 × 255 pixels, whose locations were randomly shuffled 10 times) and, as a result, their content was made meaningless. Thus, in total, participants were presented with 412 IAPS scenes.[1]

The selected IAPS pictures were resized to 922 × 691 pixels (90% of the original 1024 × 768 pixel size), and they were presented at the beginning of each trial (see details below). For the progressive unfolding procedure, a separate pre-processing was carried out on the original IAPS scenes (1024 × 768 pixels) (Schettino et al., 2011). First, a grayscale conversion was applied using the algorithm included in Adobe Photoshop 6.0 (Adobe Systems, Mountain View, CA). Afterwards, six bandpass spatial frequency filters were applied on each and every picture using the fast Fourier transform (FFT) included in ImageJ v1.44 (http://rsb.info.nih.gov/ij/; for a similar procedure, see Delplanque et al., 2007). As a result, six distinct levels of filtering were obtained for every IAPS scene, each containing a different amount of low and high spatial frequency information.[2] All these modified pictures were finally resized to 768 × 576 pixels (75% of

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[1] See Schettino et al. (2012) for a complete list of the IAPS pictures selected for the experiment.

[2] *Image1*: 256–1024 pixels/cycles; *Image2*: 128–1024 pixels/cycles; *Image3*: 64–1024 pixels/cycles; *Image4*: 32–1024 pixels/cycles; *Image5*: 16–1024 pixels/cycles; *Image6*: 0–1024 pixels/cycles. The numbers in the pair denote the pixels between which the cycles were kept after FFT (Delplanque et al., 2007).

the original IAPS pictures). Importantly, the grayscale and resize picture conversions relative to the colorful picture were performed to discourage participants to use a purely perceptual, pixel-to-pixel matching strategy to retrieve the content of the initial picture during the memory matching task (see Procedure below).

Each neutral, unpleasant, and pleasant scene was arbitrarily paired with another one from the same emotion category based on low-level visual similarities, as assessed by systematic visual inspection (see Table 2 in Schettino et al., 2012). More specifically, pictures with a clear distinction between a central figure and a homogeneous background were paired together (e.g., a coffee mug on a table vs. a pocket watch on a dark background). The same strategy was applied for more complex scenes (e.g., a traffic jam vs. a woman in the crowd). Of note, this procedure was applied on the fourth image level of each IAPS scene (*Image4*), given that the behavioral results of our previous study (Schettino et al., 2011) showed that participants could reliably recognize these complex visual scenes using the spatial frequency information content provided in this specific image level.

Procedure

Participants were individually tested in a small, dimly lit room, and seated at a viewing distance of 75 cm in front of a 19″ CRT computer screen (refresh rate: 100 Hz). After filling out the informed consent, they were presented with task instructions, followed by a practice block containing 16 trials (with neutral pictures). Then, they moved on to the main experimental session, which was divided into twelve blocks (separated by short breaks), each containing 33 trials (Schettino et al., 2012; see also Fig. 1A). Each trial began with a 1500 ms presentation of a colorful, fully detailed picture subtending 18.5° × 13.9° of visual angle, followed by a 2000 ms grayscale mask. At the offset of the mask, the unfolding sequence started. A fixation cross appeared in the center of the screen for 250 ms. The first grayscale, blurred image level of a given picture (subtending 15.4° × 11.6° of visual angle) was then presented for 500 ms, followed by a 250 ms blank screen. Next, the second image level of the same picture (containing slightly more HSF and LSF information) was displayed for 500 ms, plus the 250 ms blank screen, and the same procedure was repeated until the presentation of the sixth, non-filtered image level. The inter-trial interval was set at 1000 ms. Participants were required to provide two separate and consecutive manual responses (see also Schettino et al., 2011, for a similar dual response procedure). First, they were asked to press, with their right index finger, a pre-defined button on a response box (Cedrus RB-730; http://www.cedrus.com/responsepads/rb730.htm) as soon as they gathered enough perceptual evidence to decide whether the content of the unfolded scene was either the same as the one displayed during the encoding phase, a new one, or a scrambled picture (Response1).[3] Pressing the button immediately interrupted the presentation of the stimulus sequence. Although instructions emphasized accuracy, participants were encouraged to stop the sequence as soon as they felt they could recognize the content of the scene, which occurred before the end of the sequence for a vast majority of trials (see Schettino et al., 2012). After 500 ms, participants were required to validate their Response1 by pressing, on a standard AZERTY keyboard, the "o" key if the unfolded scene was the same as the colorful one previously presented ("old" condition), the "n" key if these two scenes were different ("new" condition), or the "s" key if the unfolded scene was displaying a meaningless content ("scrambled" condition). All these responses, for which no time limit was imposed, were coded as Response2. This dual response procedure was used for three main reasons: (i) to dissociate early visual recognition effects (Response1) from the overt discrimination and comparison in short-term memory of the scenes (Response2); (ii) to remove recognition errors (based on accuracy of Response2) from the behavioral and ERP analyses; and (iii) to minimize the potential contamination of ERP data by the activation of competing motor responses across the three different conditions, since Response1 always required to press a single button shared across conditions. To further prevent the use of a recognition strategy solely based on low-level visual features, the content of half of the "old" scenes was unpredictably flipped along the horizontal axis between encoding and retrieval. Participants were informed that an "old" response was to be given for these "flipped" trials, since the memory matching task had to be performed primarily based on the *content* of the scenes. For the statistical analyses of the behavioral and EEG data reported hereafter, "old flipped" and "old unflipped" trials were combined into a single "old" condition, and these "old" trials were eventually compared to "new" trials (see also Schettino et al., 2012). Hence, using this procedure, for each emotion category (neutral, pleasant, unpleasant), two trial types were compared to each other: "old", in which the identity of the colorful picture was identical to the scene progressively unfolded; "new", meaning that the identities of the colorful and unfolded scene were different (although matched as far as possible in terms of low-level visual properties). Importantly, for "new" scenes, no change in terms of emotional content ever occurred between the colorful picture and the gradually unfolded scene. In other words, a neutral colorful picture was always followed by the unfolding of a neutral scene, and the same occurred for emotion-laden stimuli (pleasant–pleasant; unpleasant–unpleasant; see Table 2 in Schettino et al., 2012).

Finally, we aimed at increasing the task-relevance of the emotional features of the scenes presented throughout the experiment, in order to increase the likelihood to find reliable differences at the electrophysiological level between emotional and neutral scenes. Therefore, additional ratings of the emotional valence of the colorful scene presented at the beginning of each trial were occasionally asked after the registration of Response2. A standard 9-point Self-Assessment Manikin (SAM; Bradley and Lang, 1994) was used for this purpose, with anchor 1 corresponding to "very unpleasant" and anchor 9 to "very pleasant". This additional emotion classification task, included in 10% of the total number of trials, also served as additional verification that the emotional content of the IAPS pictures selected in our study was perceived by our participants in accordance with the normative ratings (Lang et al., 2008).

Stimulus presentation and behavioral response recordings were controlled using E-Prime 2.0 (http://www.pstnet.com/products/e-prime/).

Recording and pre-processing of EEG data

Electroencephalographic (EEG) activity was continuously recorded using a BIOSEMI Active-Two system (BioSemi, Inc., The Netherlands; http://www.biosemi.com) by means of 128 Ag/AgCl electrodes fitted into a stretching cap and following the BioSemi ABCD position system (i.e., electrode positions are radially equidistant from CZ; http://www.biosemi.com/headcap.htm). Two additional electrodes, the common mode sense (CMS) active electrode and the driven right leg (DRL) passive electrode, were used as reference and ground electrodes, respectively (http://www.biosemi/faq/cms_and_drl.htm). Vertical electrooculograms (vEOG) were monitored using two additional electrodes placed on the inferior and superior areas of the left orbit, whereas horizontal EOG (hEOG) were recorded by means of two electrodes situated symmetrically on the outer canthus of each eye. EEG and EOG recordings were sampled at 512 Hz.

ERPs of interest were computed offline using Brain Vision Analyzer 2.0 (Brain Products™ GmbH, Munich, Germany; www.brainproducts.com). First, a topographic interpolation (interpolation by spherical splines; Perrin et al., 1989) was applied on noisy channels (interpolated channels across 18 subjects: $M = 3.78$, $SD = 4.28$, range 0–11), and a common average reference was then applied. Afterwards, the continuous EEG signal was segmented into individual epochs, excluding trials

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[3] These scrambled pictures, for which a separate response was required, were used as "catch" trials to ensure that participants reliably attended to the content of the scenes before responding, as well as an additional control to prevent the use of a strategy primarily based on the detection of specific low-level details.

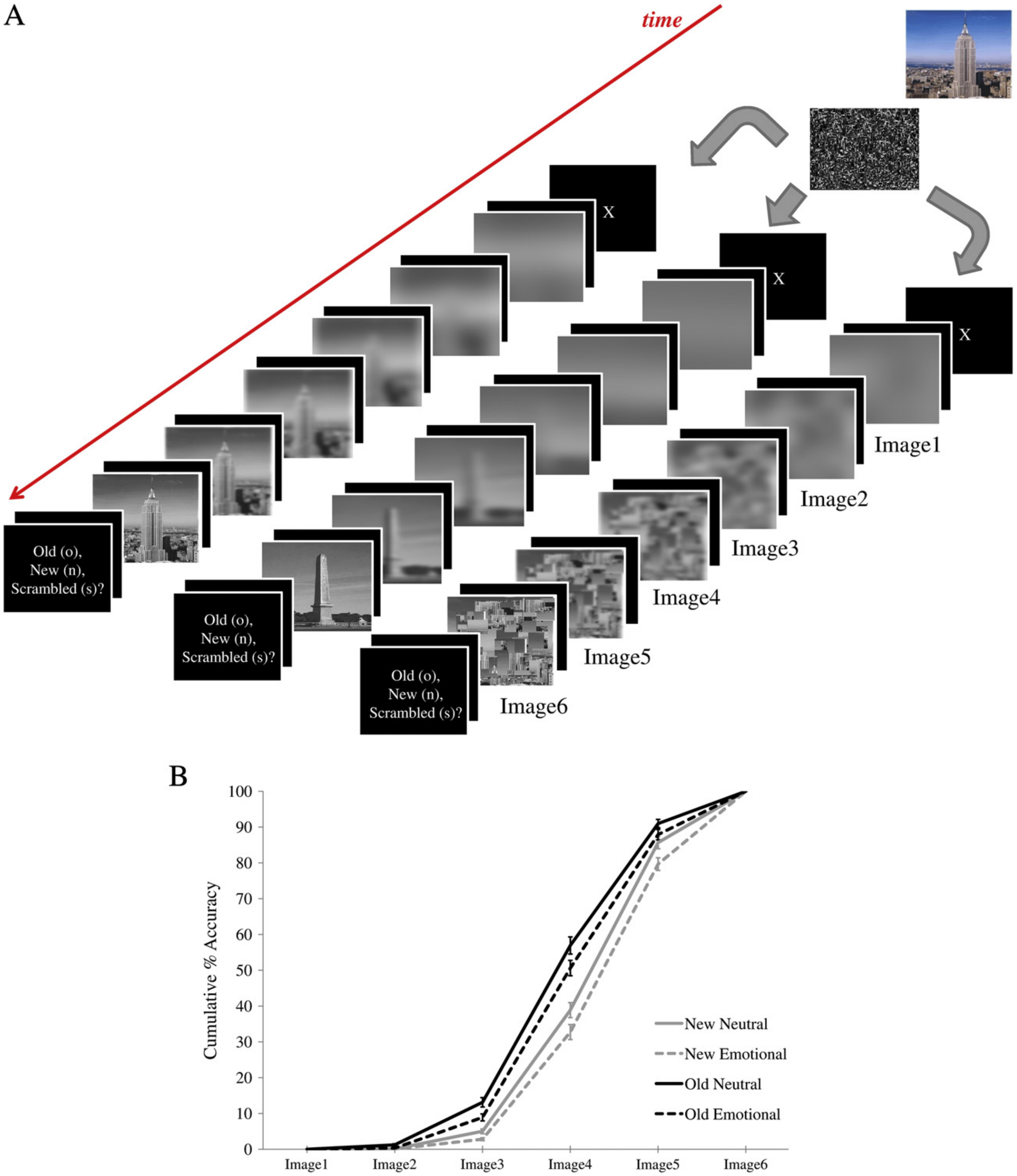

Fig. 1. (A) Procedure and task. Colorful neutral, unpleasant, and pleasant IAPS scenes (not shown here for copyright reasons) were randomly presented to participants at the beginning of each trial. After a mask, a grayscale version of the same scene, a new one, or a scrambled picture was progressively revealed using six sequential steps. Each step added new low and high spatial frequency information to the previous one, in a parametric fashion. Participants were required to stop the sequence – by pressing a button on the response box (Response 1) – as soon as they could decide whether the content of the gradually unfolded scene was the one seen at the beginning of the trial (i.e., colorful picture), a new one, or a scrambled picture. Participants subsequently validated their choice and confirmed whether the scene was "old", "new", or "scrambled" (Response 2). (B) Behavioral results. Cumulative percentage of correct Responses1 as a function of the six image levels, separately for new (gray lines), old (black lines), neutral (solid lines), and emotional (dashed lines) scenes. Vertical bars correspond to standard errors of the mean. Results show that participants were able to perform the memory task significantly earlier for old relative to new scenes, suggesting that less perceptual evidence was needed for the former compared to the latter. Neutral scenes were recognized reliably earlier compared to emotional scenes. No significant interaction effect between memory and emotion was found (see main text).

corresponding to errors (based on accuracy on Response2). Similar to our previous study (Schettino et al., 2011), four main epochs were computed around stimulus onset (using an interval of 200 ms prior to and 750 ms after this event), enabling us to look backwards at visual ERPs progressively elicited prior to Response1: (1) segments in which Response1 occurred from 0 to 750 ms after stimulus presentation ("recognition"); (2) segments in which Response1 occurred from 750 to 1500 ms after stimulus presentation ("one image before" recognition); (3) segments in which Response1 occurred from 1500 to 2250 ms after stimulus presentation ("two images before" recognition); (4) segments in which Response1 occurred from 2250 to 3000 ms after stimulus presentation ("three images before" recognition). A segment length of 750 ms was used in order to include stimulus presentation duration (500 ms) as well as the following 250 ms blank screen. These parameters minimized the possibility that late ERPs for the preceding image level could substantially contaminate the pre-stimulus baseline of the current image level (see Figs. 3 and 4A). All these individual segments were then baseline corrected using the entire pre-stimulus interval of 200 ms, before a standard ocular correction was performed (Gratton et al., 1983). Artifact rejection was then carried out ($-80/+80$ μV amplitude scale across participants) to remove segments contaminated by artifacts, including residual eye blinks and muscle activity. Finally, stimulus-locked ERP averages were computed, separately for each condition (memory: 2 levels; emotion: 3 levels; recognition times: 4 levels), resulting in 24 individual ERP averages. However, because no difference in recognition between unpleasant and pleasant pictures was observed at the behavioral level (see also Schettino et al., 2012), these two emotion conditions were collapsed in order to increase the signal-to-noise ratio, leaving a total number of 16 individual ERP averages (percentage of segments kept after pre-processing: ~79%).[4] These averages were eventually low-pass filtered using a 30 Hz cutoff (slope 12 dB/oct).

To provide additional evidence for the overt processing of the emotional dimension of the stimuli, we used a standard ERP marker of emotional processing. More specifically, in an auxiliary analysis, we computed visual ERPs time-locked to the onset of the colorful picture (epoch length: $-200/+1500$ ms) that was presented at the beginning of the trial and had to be encoded in short-term memory. We sought to establish whether emotional scenes were perceived and processed differently compared to neutral scenes, as indicated by a larger LPP amplitude for emotional relative to neutral scenes (Foti et al., 2009; Schupp et al., 2003, 2004a,2004b, 2006).

Analysis of ERP data

First, we analyzed the average amplitude of the LPP component time-locked to the onset of the colorful scene – extracted from a 500–1000 ms time window following stimulus onset – from an array of centro-parietal electrodes, where this component reached its maximum amplitude. Mean amplitudes of the LPP were analyzed by means of repeated measures ANOVAs, and *t*-tests were employed as post-hoc comparisons.

Second, to investigate the classical old/new effect (Rugg and Curran, 2007; Voss and Paller, 2008; Wilding et al., 1995), we analyzed the average amplitude of the centro-parietal ERP component (recorded from electrode A19, which corresponds to Pz in the 10/20 international EEG system) time-locked to the time of recognition, and extracted from a 500–750 ms time window post-stimulus onset (Paller et al., 2003; Voss and Paller, 2006).[5] Paired-samples *t*-tests were used to verify a mean amplitude difference of this late positive potential between old and new scenes.

To examine the ERP data recorded during the progressive unfolding sequence, reference-free topographic analyses were used, similarly to our previous study (Schettino et al., 2011). This method allows to summarize a complex ERP data set into a smaller number of dominant scalp topographies (i.e., global configuration of the electric field across all 128 channels at each time frame) (Lehmann and Skrandies, 1980; Michel and Murray, 2012; Michel et al., 1999, 2001; Murray et al., 2008; Pourtois et al., 2008). These analyses enable to assess how the distribution and expression of these dominant topographies vary in time across experimental conditions, irrespective of changes in the strength of the ERP signal. Topographic analyses were performed using CARTOOL software (version 3.43; http://brainmapping.unige.ch/Cartool.htm; see also Brunet et al., 2011). The dominant scalp maps were identified in the grand-average ERP data for each main condition (recognition, one image before, two images before, and three images before) over a wide time window spanning from 0 to 600 ms after stimulus onset. To this end, a specific spatiotemporal clustering algorithm, the "Atomize and Agglomerate Hierarchical Clustering" (AAHC; for a detailed description, see Murray et al., 2008; Tibshirani and Walther, 2005), was used. The optimal number of dominant maps best "explaining" the ERP dataset was determined, following standard practice, using a cross-validation criterion (Pascual-Marqui et al., 1995). Next, the spatial correlation between single-subject ERPs and the aforementioned template maps identified by the AAHC clustering algorithm was calculated (a procedure called "fitting"; Brandeis et al., 1995; Murray et al., 2008), in order to obtain a quantitative estimate of each map's relative expression across subjects and conditions, as defined by the global explained variance (GEV, or goodness of fit). GEV values were entered in repeated measures ANOVAs, with recognition level, memory, and emotion as within-subject factors. Paired *t*-tests were used as post-hoc comparisons between conditions, when required to back up significant interaction effects. Whenever Mauchly's test indicated that the assumption of sphericity had been violated, the degrees of freedom were corrected using Greenhouse-Geisser estimates. The alpha level was set at $p < 0.05$.

Source localization analysis

To estimate the putative neural generators underlying the dominant voltage topographies identified at the scalp level by the previous analyses, we used sLORETA (Pascual-Marqui, 2002). sLORETA is a distributed linear inverse solution based on the neurophysiological assumption of coherent co-activation of neighboring cortical areas, known to have highly synchronized activity (Silva et al., 1991). Accordingly, it estimates multiple simultaneously active sources without any a priori assumption on the number and position of the underlying dipoles (for a mathematical validation of this localization technique, see Sekihara et al., 2005). sLORETA solutions are computed within a three-shell spherical head model co-registered to the MNI152 template (Mazziotta et al., 2001), restricted to the gray matter and the hippocampus. The source locations were therefore given as (x, y, z) coordinates (x from left to right; y from posterior to anterior; z from inferior to superior). The estimation of the three-dimensional intracerebral current density distribution is performed in 6239 voxels, each containing an equivalent current dipole. The head model for the inverse solution uses the electric potential lead field computed with a boundary element method applied to the MNI152 template (Fuchs et al., 2002). Scalp electrode coordinates on the MNI brain are derived from the international 5% system (Jurcak et al., 2007). The calculation of all reconstruction parameters was based on the computed common average reference.

sLORETA units were scaled to amperes per square meter (A/m^2), normalized across subjects, and nonparametric statistics were then applied on log-transformed data. Direct statistical comparisons between conditions were performed in this inverse solution space using repeated

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[4] Number of segments after pre-processing, separately for each condition: (1) new, recognition, neutral: $M = 52$, range 44–58; (2) new, recognition, emotional: $M = 103$, range 78–114; (3) old, recognition, neutral: $M = 47$, range 34–58; (4) old, recognition, emotional: $M = 90$, range 68–111; (5) new, one image before, neutral: $M = 50$, range 41–59; (6) new, one image before, emotional: $M = 103$, range 83–116; (7) old, one image before, neutral: $M = 41$, range 30–52; (8) old, one image before, emotional: $M = 87$, range 68–106; (9) new, two images before, neutral: $M = 52$, range 40–58; (10) new, two images before, emotional: $M = 104$, range 81–116; (11) old, two images before, neutral: $M = 47$, range 37–58; (12) old, two images before, emotional: $M = 90$, range 74–111; (13) new, three images before, neutral: $M = 49$, range 37–57; (14) new, three images before, emotional: $M = 100$, range 76–115; (15) old, three images before, neutral: $M = 41$, range 32–52; and (16) old, three images before, emotional: $M = 84$, range 67–105.

[5] As a control analysis, we also calculated the mean amplitude of the old/new ERP effect recorded from an array of parietal electrodes located in the left (A5, A6, A7, A8, D16, D17, D27, D28) and right (A31, A32, B2, B3, B4, B17, B18, B19) hemispheres (Curran and Doyle, 2011; Weymar et al., 2009; Wilding et al., 1995)(Curran and Doyle, 2011; Weymar et al., 2009; Wilding et al., 1995), and we obtained a similar statistical outcome. Therefore, for ease of presentation, only the results of Pz are reported.

measures ANOVAs and post-hoc paired *t*-tests. The level of significance for all these analyses was set at $p < 0.05$.

Results

Emotion classification task

Results of the emotion classification task showed high (i.e., more pleasant) ratings for pleasant ($M = 6.14$, $SD = 0.81$) scenes, followed by neutral ($M = 4.89$, $SD = 0.58$) and unpleasant ($M = 3.45$, $SD = 1.06$) scenes. A one-way ANOVA performed on these mean ratings disclosed a highly significant effect of emotion [$F(2, 34) = 39.94$, $p < .001$, $\eta_p^2 = .701$]. Paired samples *t*-tests carried out on these mean ratings confirmed highly significant differences between neutral and unpleasant pictures [$t(17) = 4.83$, $p < .001$], as well as between neutral and pleasant [$t(17) = -7.47$, $p < .001$] and unpleasant and pleasant [$t(17) = -6.81$, $p < .001$] scenes. Thus, participants rated the emotional valence of the pre-selected stimuli in accordance with the published normative scores (Lang et al., 2008). These results also confirmed that participants correctly attended to the actual emotional content of the scenes throughout the experiment.

Accuracy for the progressive unfolding task

Cumulative percentages of correct responses (i.e., Responses1 only when Responses2 were correct) are shown in Fig. 1B (for a detailed overview, see Schettino et al., 2012). A mixed proportional odds model with memory (old, new) and emotion (neutral, emotional) as fixed factors, and participant as random effect revealed an overall earlier recognition for old compared to new scenes, in both neutral and emotional conditions (all *ps* $< .001$). Interestingly, pairwise comparisons revealed a shift of the psychometric curve as a function of the emotional content of the scene, indicated by an earlier recognition when the scenes contained a neutral as opposed to an emotional content (all *ps* $< .01$). No significant interaction effect was found between memory and emotion ($p = .632$).

LPP during stimulus encoding

Fig. 2 shows the grand-average ERPs recorded from an array of medial centro-parietal electrode sites (A8, A20, B5). These electrodes were selected for illustration purposes after an initial 2 (emotion) × 9 (electrode) repeated measures ANOVA revealed no significant interaction effect between these two factors ($p > .05$). The analysis performed on the mean amplitude of the LPP showed a larger sustained positive component for emotional ($M = 5.86$ μV, $SD = 4.32$) relative to neutral ($M = 4.91$ μV, $SD = 4.47$) scenes. Paired *t*-tests confirmed a significant amplitude difference between neutral and emotional scenes [$t(17) = -3.75$, $p = .002$]. Thus, these results provided additional evidence for the differential processing of the emotional content of the scenes encoded in short-term visual memory prior to unfolding. We also performed correlation analyses between the LPP amplitude and task performance (i.e., memory accuracy during the progressive unfolding task), separately for new, old, neutral, and emotional scenes. However, no significant correlation was observed (all *ps* $> .05$).

Old/new ERP effects at time of recognition

The time course of the centro-parietal old/new ERP component recorded at time of recognition is shown in Fig. 3. The analysis performed on the mean amplitude of this component (measured in a 500–750 ms time window post-stimulus onset) showed significantly larger positive values for old ($M = 1.44$ μV, $SD = 2.41$) relative to new ($M = 0.40$ μV, $SD = 1.77$) scenes [$t(17) = -3.04$, $p = .007$]. These results are consistent with previous ERP studies (Curran and Cleary, 2003; Curran and Doyle, 2011; Sanquist et al., 1980; Wilding and Rugg, 1996; Wilding et al., 1995), and provide converging evidence that our short-term memory manipulation was successful.

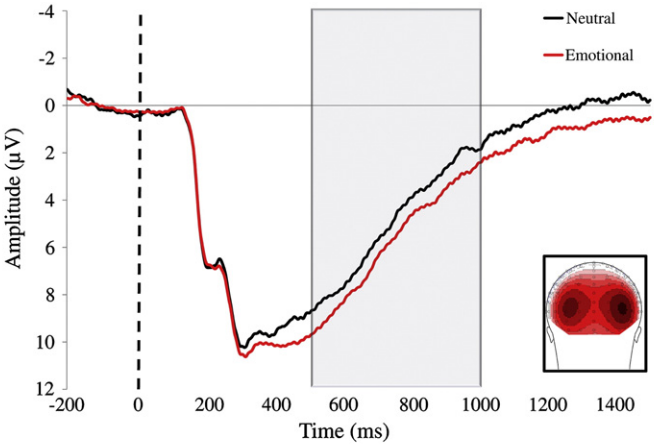

Fig. 2. Grand-average LPP recorded from a posterior parietal cluster of electrodes (average of activity recorded from electrodes A8, A20, B5), separately for neutral (black line) and emotional (red line; pleasant and unpleasant merged) scenes. The black vertical dashed line indicates the onset of the colorful picture. The gray area indicates the time window during which the mean amplitude of the LPP was measured (500–1000 ms post-stimulus onset). LPP was significantly larger for emotional compared to neutral scenes.

Topographic analysis of ERPs recorded during the unfolding task

The spatiotemporal cluster analysis revealed that eight distinct dominant field topographies explained 91.34% of the total variance (see Figs. 4A and B). Similarly to our previous study (Schettino et al., 2011), we found a reliable topographical change across recognition levels immediately following the exogenous N1 and P2 ERP components (Fig. 4B).[6] Because this topographical alteration necessarily indicates changes in the configuration of the underlying intracranial generators (Lehmann and Skrandies, 1980; Michel and Murray, 2012), a detailed characterization of this topographical change starting ~400 ms following stimulus onset is provided.

At the offset of the P2 scalp map, for three, two, and one images before recognition, an occipital positivity with a concurrent, broad frontal negativity was evidenced. Conversely, an occipital positivity accompanied by a more focal frontal positivity was observed one image before recognition, being then predominant at time of recognition (Fig. 4B). These two distinctive dominant topographical components were then fitted back to the individual ERP data. Based on the outcome of the spatiotemporal analysis, we selected a large time interval lasting 120 ms, namely from 402 to 522 ms after stimulus onset, during which these topographic differences were most obvious (Fig. 4B). A 2 (map configuration: occipital positivity/frontal negativity, occipital positivity/frontal positivity) × 4 (recognition level: recognition, one image before, two images before, three images before) repeated measures ANOVA on the GEV values obtained for these two specific topographies after fitting revealed significant main effects of map configuration [$F(1, 17) = 7.40$, $p = .015$, $\eta_p^2 = .303$] and recognition level [$F(3, 51) = 10.69$, $p < .001$, $\eta_p^2 = .386$], as well as a highly significant map configuration × image level interaction [$F(3, 51) = 9.53$, $p < .001$, $\eta_p^2 = .359$]. Interestingly, pairwise comparisons showed that the GEV of the occipital positivity/frontal positivity map progressively increased from three images before recognition to actual recognition (all *ps* $< .05$, except two images vs. three images before recognition, $p = .079$) (see Fig. 4D). By comparison, the GEV of the occipital positivity/frontal negativity showed a different pattern (Fig. 4C). Paired *t*-tests revealed a sharp increase in GEV from

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[6] No difference in GEV was found for the N1 and P2 scalp topographies as a function of time of recognition. Therefore, these early maps will not be discussed further.

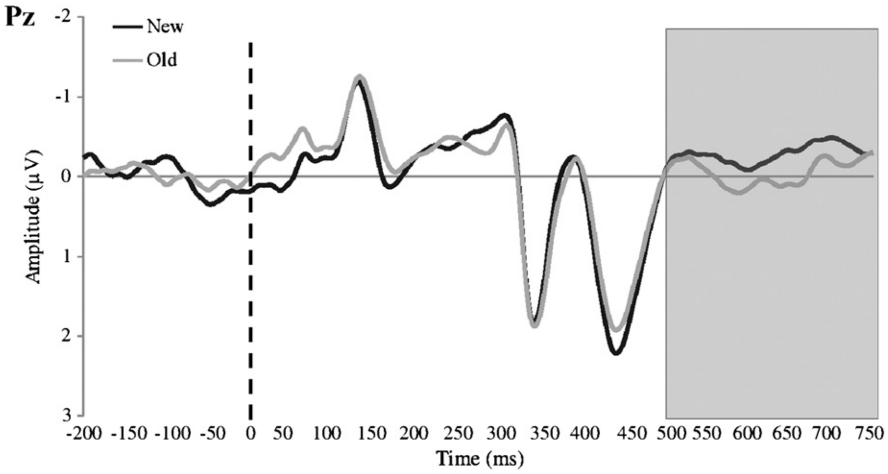

Fig. 3. Grand-average ERP (at electrode A19/Pz) showing the classical old/new effect (new scenes: black line; old scenes: gray line). A 0.5 Hz high-pass filter has been applied for visualization purposes. The black vertical dashed line indicates the onset of the picture that was subsequently recognized (time of recognition). The gray area indicates the time window during which the mean amplitude of this centro-parietal positive component was measured (500–750 ms post-stimulus onset). Amplitude values were more positive for correctly recognized old scenes compared to correctly recognized new scenes, in line with previous ERP studies.

three to two images before recognition [$t(17) = -3.88$, $p = .001$], followed by a gradual decrease between two images before and time of recognition [$t(17) = 3.21$, $p = .005$], as well as between one image before and actual recognition [$t(17) = 2.67$, $p = .016$]. Thus, this latter topographical scalp map explained most of the variance already two images before recognition, but then gradually decreased and was replaced by the concurrent occipital positivity/frontal positivity.

Next, we investigated whether these two dominant topographical maps were differentially influenced by memory, emotional content, or both factors concurrently. Regarding the occipital positivity/frontal negativity topography, a 2 (emotion) × 2 (memory) × 4 (recognition level) repeated measures ANOVA showed a significant memory × recognition level interaction [$F(3, 51) = 3.28$, $p = .028$, $\eta_p{}^2 = .162$], but no significant effect of emotion [$F(1, 17) = 1.01$, $p = .330$, $\eta_p{}^2 = .056$]. A similar 2 × 2 × 4 ANOVA on the GEV values of the occipital positivity/frontal positivity map disclosed a significant main effects of memory [$F(1, 17) = 20.30$, $p < .001$, $\eta_p{}^2 = .544$], and a memory × recognition level interaction [$F(3, 51) = 3.36$, $p = .026$, $\eta_p{}^2 = .165$] but no significant effect of emotion [$F(1, 17) = 0.29$, $p = .596$, $\eta_p{}^2 = .017$].

Given the lack of statistical significance for the emotion factor, we collapsed GEV values for neutral and emotional scenes and further investigated the modulatory role of memory. A 2 (memory) × 4 (recognition level) repeated measures ANOVA on the GEV values of the occipital positivity/frontal negativity map disclosed a significant memory × recognition level interaction [$F(3, 51) = 3.28$, $p = .028$, $\eta_p^2 = .162$]. Post-hoc comparison showed higher GEV for new compared to old condition two images before recognition [$t(17) = 2.52$, $p = .022$] (Fig. 4C). Thus, this analysis revealed a similar pattern of activity in new and old conditions for this occipital positivity/frontal negativity topographical map, with higher GEV values for new relative to old conditions two images before recognition.

A comparable 2 × 4 ANOVA was used for the GEV values obtained for the concurrent occipital positivity/frontal positivity topography. This analysis showed a significant main effect of memory [$F(1, 17) = 20.30$, $p < .001$, $\eta_p{}^2 = .544$], as well as a significant memory × recognition level interaction [$F(3, 51) = 3.36$, $p = .026$, $\eta_p{}^2 = .165$]. Post-hoc paired *t*-test revealed higher GEV values for new relative to old conditions, both one image before [$t(17) = 3.41$, $p = .003$] and at recognition level [$t(17) = 4.12$, $p = .001$] (Fig. 4D). Thus, a comparable, gradual increase in GEV was observed for new and old scenes, with higher values for new relative to old condition one image before, as well as at time of recognition.

Source localization results

Using sLORETA (Pascual-Marqui, 2002) we performed statistical non-parametric mapping (SnPM) analyses on the average activity estimated during the 402–522 ms post-stimulus onset interval, during which the main topographic change took place across the four recognition levels (from three images before up to recognition). We first compared ERP activity for three images before recognition to actual recognition (see Schettino et al., 2011, for a similar approach), separately for new and old scenes. This analysis revealed, for new scenes, a stronger activation for recognition relative to three images before in the dACC ($\pm 10x$, $+15y$, $+35z$) [$t(17) = 2.75$, $p = .014$], whereas symmetrically stronger activity three images before compared to recognition was found in the insula ($\pm 40x$, $+15y$, $0z$) [$t(17) = -3.29$, $p = .004$] (Fig. 5, upper panel). On the other hand, the SnPM analysis for old scenes showed stronger activity during recognition relative to three images before recognition in a non-overlapping network of brain regions, including the PHG ($\pm 29x$, $-49y$, $-6z$) [$t(17) = 4.46$, $p < .001$] and the fusiform gyrus (FG; $\pm 41x$, $-45y$, $-19z$) [$t(17) = 4.02$, $p = .001$] (Fig. 5, lower panel). Therefore, these four brain areas (dACC, insula, PHG, and FG) were defined as regions of interest (ROIs) for further analyses.[7] For each ROI (defined as a sphere of 5 mm radius centered around the coordinates reported above), we extracted the mean amplitude (current density) value during the same time interval (402–522 ms following stimulus onset) and assessed, at the statistical level, effects of recognition level and emotion.

dACC and insula (new scenes)

Regarding the dACC (Fig. 6A), the 2 (emotion) × 4 (recognition level) ANOVA performed on the mean current density extracted during the 402–522 ms interval post-stimulus onset revealed a significant main effect of recognition level [$F(3, 51) = 5.84$, $p = .002$, $\eta_p{}^2 = .256$]. Post-hoc *t*-tests revealed higher activity for late vs. early recognition levels, as evidenced by a significant difference between two images and one image before recognition [$t(17) = -2.74$, $p = .014$]. Activity remained stable between three images and two images before recognition, as well as between one image before and time of recognition ($ps > .05$) (Fig. 6A).

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[7] None of these ROIs showed differential lateralization effects, as confirmed by 2 (side) × 4 (recognition level) repeated measures ANOVAs. Accordingly, for each ROI, activity from both hemispheres was combined.

Inverse solution results obtained for the insula in the new condition revealed a similar response profile (Fig. 6B). However, the emotional content of the scenes visibly influenced reconstructed activity in this ROI, unlike the dACC. A 2 (emotion) × 4 (recognition level) ANOVA disclosed a significant emotion × recognition level interaction [$F(3,\ 51) = 3.75$, $p = .016$, $\eta_p{}^2 = .181$]. Post-hoc analyses showed, for neutral pictures, only a significant difference between three images before and time of recognition [$t(17) = -2.34$, $p = .032$]. Therefore, activity in the insula for neutral pictures was relatively stable until recognition. By contrast, emotional scenes elicited significantly higher activity one image relative to two images before recognition [$t(17) = -3.17$, $p = .006$]. Activity remained stable between three images and two images before recognition, as well as between one image before and time of recognition ($ps > .05$) (Fig. 6B).

PHG and FG (old scenes)

The response profile of the PHG and FG during recognition of old scenes was reliably different compared to the two previous ROIs

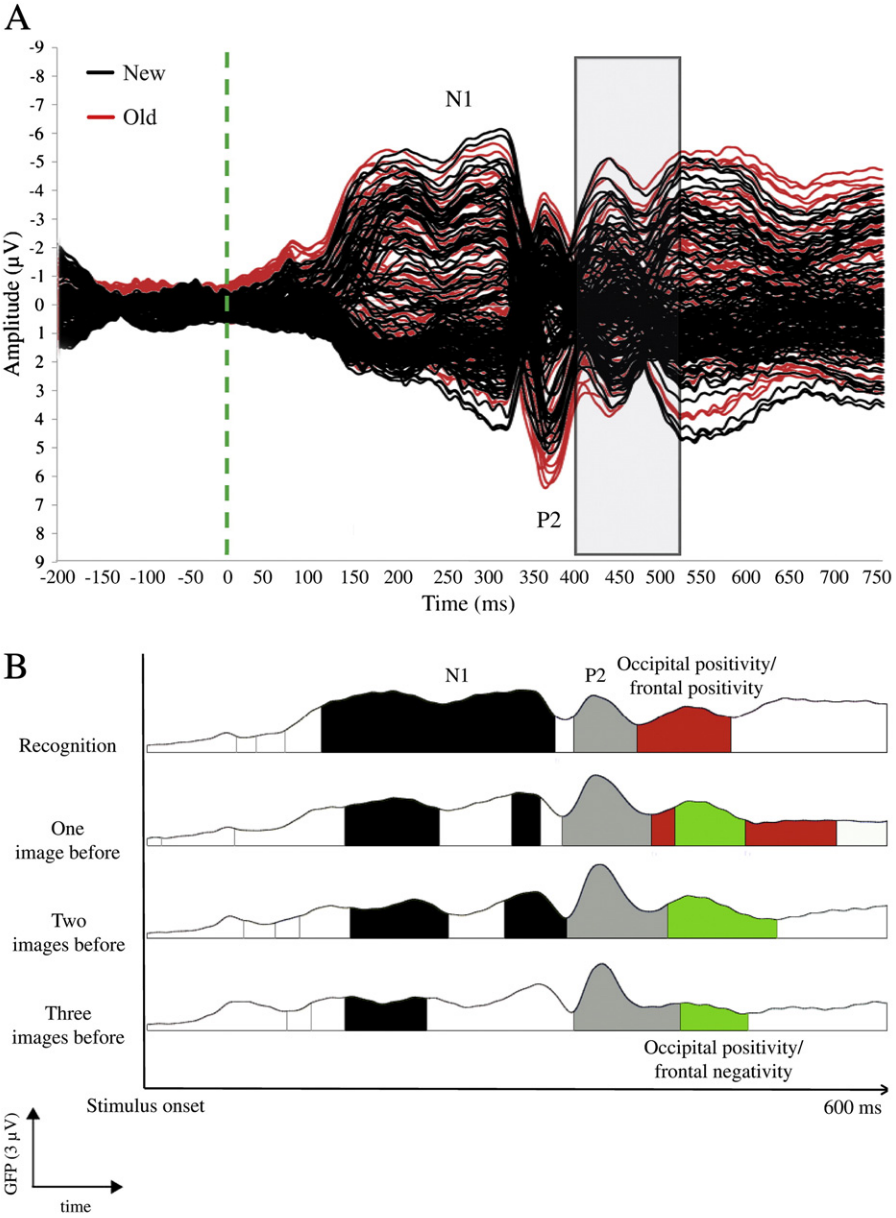

Fig. 4. Topographic mapping results. (A) Grand-average ($N = 18$) ERP waveforms, obtained for the level corresponding to actual recognition (new scenes in black, old scenes in red), for all 128 electrodes concurrently (butterfly). The green dashed vertical line indicates the onset of the visual stimulus. The gray area indicates the time window (400–522 ms) during which a reliable topographical change occurred. (B) Results of the spatiotemporal cluster analysis (0–600 ms after stimulus onset) for the four main conditions (recognition, one image before, two images before, and three images before recognition). A main solution with eight dominant topographic maps was found to explain >90% of the variance (for illustrative purposes, only the most salient maps are highlighted). Scalp topographies of the N1 (in black) and P2 (in gray) ERP components were shared across the four conditions, suggesting a similar low-level processing of the visual stimulus. By contrast, in a time window spanning 402–522 ms following stimulus onset, reliable topographic changes were observed between the four recognition levels. An occipital positivity with a broad frontal negativity (in green) explained most of the variance up to one image before recognition. Conversely, an occipital positivity with a focal frontal positivity (in red) was already evidenced one image before recognition, being then predominant at time of recognition. (C) Statistical results, obtained after the fitting procedure, for the GEV of the occipital positivity/frontal negativity scalp map identified in the 402–522 ms time window following stimulus onset (separately for new vs. old scenes). Results showed a sharp increase in GEV from three images to two images before recognition, followed by a progressive decrease until recognition. Furthermore, a higher GEV for new relative to old scenes was evidenced two images before recognition. (D) On the other hand, a linear increase in GEV as a function of recognition level was evident for the concurrent occipital positivity/frontal positivity topography. A higher GEV was observed for new compared to old scenes one image before recognition, as well as at recognition. $^{*}\ p < .05$; $^{**}\ p < .01$; $^{***}\ p < .001$. Vertical bars correspond to standard errors of the mean.

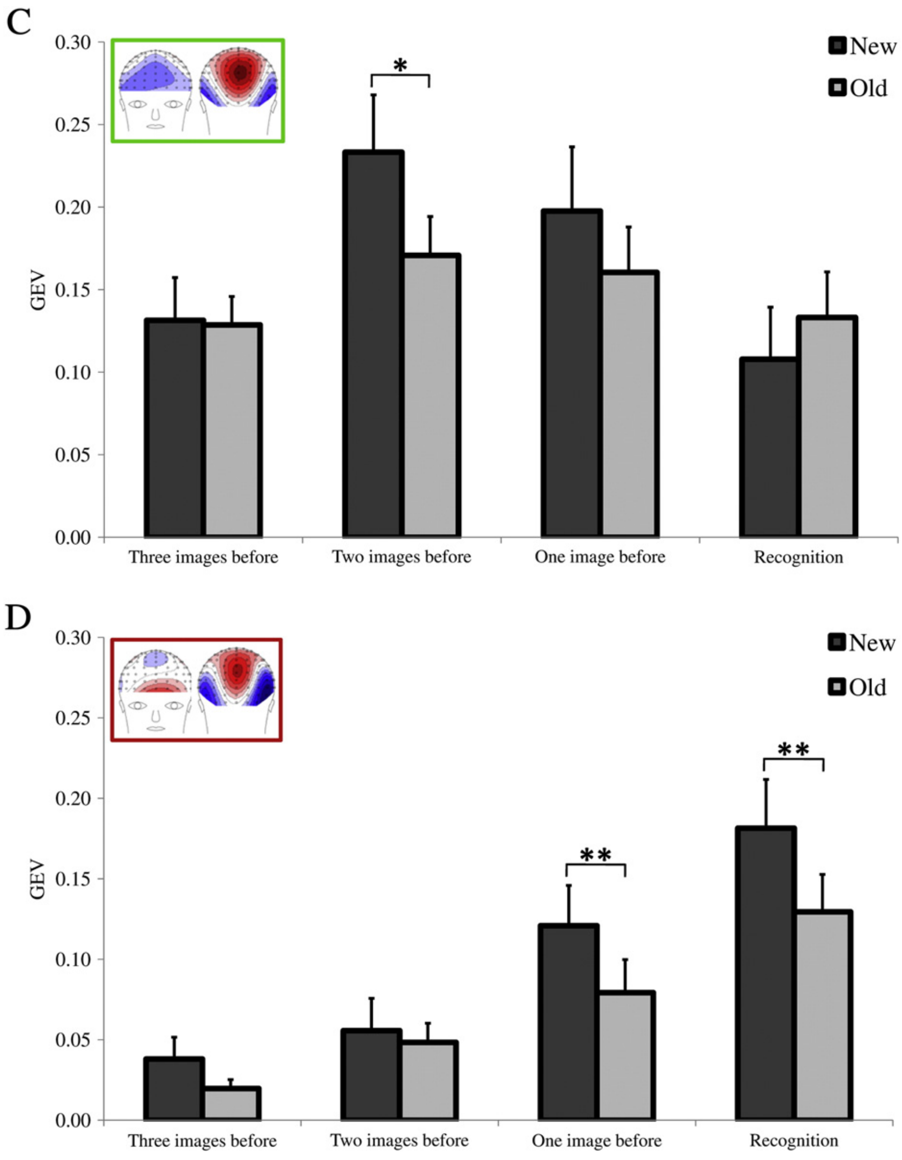

Fig. 4 (*continued*).

(i.e., dACC and insula) identified primarily for the processing of new scenes. Unlike a categorical difference between early vs. late stages of accumulation of perceptual evidence, a linear increase in current source density was observed when moving from three images before to actual recognition in the PHG and FG. A 2 (emotion) × 4 (recognition level) ANOVA on the extracted amplitude values for the PHG revealed significant main effects of emotion [$F(1, 17) = 6.33$, $p = .022$, $\eta_p{}^2 = .271$] and recognition level [$F(3, 51) = 17.06$, $p < .001$, $\eta_p{}^2 = .501$]. Post-hoc comparisons showed higher activity three images before recognition for neutral compared to emotional scenes [$t(17) = 2.96$, $p = .009$] (Fig. 6C).

The same analyses performed on the extracted amplitude values for the FG yielded comparable results. The 2 (emotion) × 4 (recognition level) ANOVA showed significant main effects of emotion [$F(1, 17) = 8.71$, $p = .009$, $\eta_p{}^2 = .339$] and recognition level [$F(3, 51) = 11.75$, $p < .001$, $\eta_p{}^2 = .409$], as well as a significant emotion × recognition level interaction [$F(3, 51) = 3.62$, $p = .019$, $\eta_p{}^2 = .176$]. As was the case for the PHG, the FG showed higher activity for neutral vs. emotional scenes three images before recognition [$t(17) = 5.62$, $p < .001$] (Fig. 6D).

Discussion

Using advanced EEG methods, we characterized the electrophysiological correlates of proactive processes active during the recognition of complex visual scenes, conveying either a neutral or an emotional (pleasant or unpleasant) content. We designed a task suited to explore the temporal dynamics of the accumulation of evidence processes, and eventually assessed whether the emotional content of the scenes could reliably modulate their expression or not. Each trial started with the presentation of a colorful neutral or emotional scene to be encoded in short-term memory, followed by the gradual unfolding of the same scene content, a new one, or a scrambled picture. Participants had to decide whether the progressively unfolded scene had the same identity as the one shown at encoding or not. Moreover, we occasionally asked participants to explicitly rate the emotional valence of the pictures, a manipulation that was meant to promote the overt processing of the emotional content of the scenes throughout the experiment. These ratings confirmed that participants correctly discriminated the emotional content of the scenes. Likewise, results obtained for the LPP component at encoding further corroborated

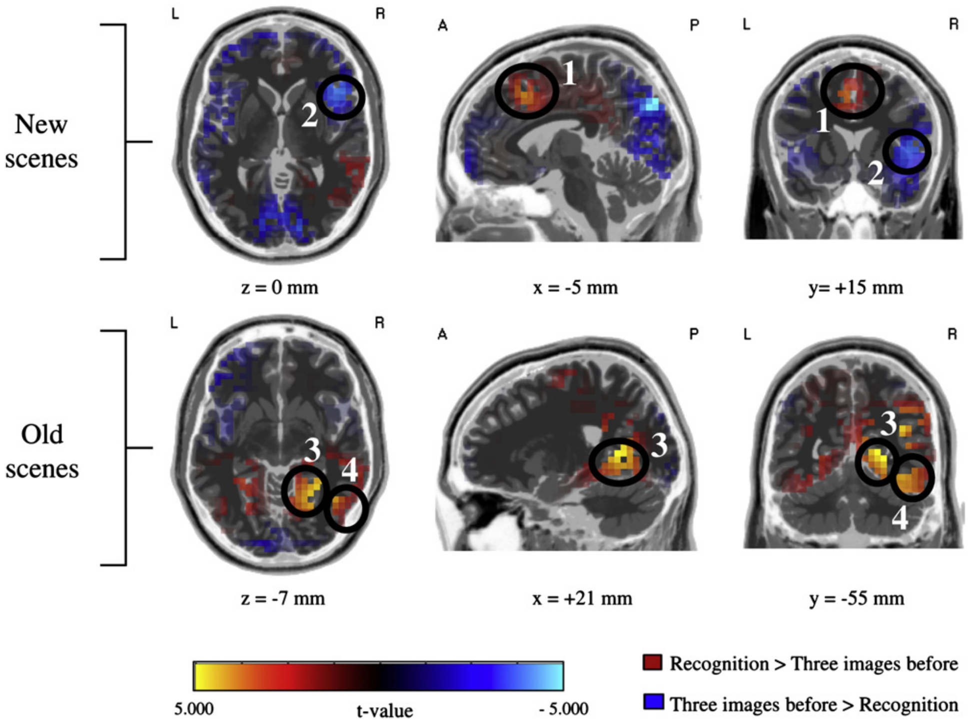

Fig. 5. Source localization results. (Upper panel) For new scenes, comparing actual recognition to three images before recognition during the 402–522 ms post-stimulus onset interval revealed a highly significant effect in the dACC (ROI # 1: $\pm 10x$, $+15y$, $+35z$). The reverse contrast (three images before vs. recognition) revealed a highly significant effect in the insula (ROI # 2: $\pm 40x$, $+15y$, $0z$). (Lower panel) For old scenes, nonparametric analyses contrasting actual recognition to three images before recognition revealed increased activity in the PHG (ROI # 3: $\pm 29x$, $-49y$, $-6z$), as well as the FG (ROI # 4: $\pm 41x$, $-45y$, $-19z$). L: left; R: right; A: anterior; P: posterior.

this conclusion (see Fig. 2). Interestingly, a number of important new results emerge from this study regarding possible modulatory effects of emotion on the online generation of guesses or predictions during overt scene recognition, as discussed here below.

Prolonged exploration for emotional compared to neutral scenes

Behavioral results revealed that old scenes were recognized systematically earlier than new scenes (Fig. 1B), providing direct evidence for the use of abstract visual representations during unfolding, which were directly shaped by information provided to participants at encoding. Moreover, we replicated our previous results (Schettino et al., 2011) and found that, regardless of the memory status of the scenes (old vs. new), participants dwelt longer on emotional compared to neutral scenes (Fig. 1B). As argued in Schettino et al. (2012), delayed recognition for emotional relative to neutral scenes could be explained by differential motivational drives between these two categories, including *positivity offset* (Cacioppo and Gardner, 1999; Cacioppo et al., 1997, 1999; Norris et al., 2010). According to this general motivational account, participants are usually inclined to engage in exploratory behavior when encountering emotion-laden stimuli (especially pleasant ones), presumably because of their intrinsic rewarding value. Interestingly, the use of mildly arousing scenes in our study, as opposed to mutilations or erotica, may have boosted this asymmetry in motivational exploratory strategies between emotional and neutral scenes. This motivational effect found in a sample of healthy women was similar for old and new scenes, suggesting that effects of emotion on proactive guesses during scene recognition probably occurred either before or after the input stimulus was compared against existing visual representations stored in (short-term) memory. Alternatively, emotion could somehow interfere with the accumulation of evidence processes (at different moments depending either on the presence or absence of an existing short-term memory trace for these scenes), in the sense that the emotional content of the scenes would exert an extra source of variability and/or uncertainty on these processes, compared to neutral scenes. In this view, the compelling processing of the emotional content of the scenes (at encoding), which is reinforced by the use of an emotion categorization task (based on the valence), leads to the activation of mental processes that are probably shared in part with brain processes responsible for the accumulation of evidence, eventually slowing down the recognition of these emotional scenes. Our new source localization results indirectly confirm this assumption (see below).

New and old scenes recruit non-overlapping brain networks during proactive visual processes

The control analysis performed on the mean amplitude of the centro-parietal old/new ERP component recorded at time of recognition in a 500-750 ms time window post-stimulus onset showed significantly larger positive values for old relative to new scenes. These results are consistent with previous studies (Curran and Cleary, 2003; Curran and Doyle, 2011; Weymar et al., 2009; Wilding and Rugg, 1996; Wilding et al., 1995), and provide converging evidence that our short-term memory manipulation was successful. However, neither the main effect of emotion nor the emotion × memory interaction was significant (all $ps > .05$), indicating comparable old/new effects for neutral and emotional scenes. This result might be explained by the use of a short retention interval in the present experimental paradigm, as opposed to previous ERP studies using intermediate (e.g., 1 week; Weymar et al., 2009, 2010) or long (e.g., 1 year; Bradley et al., 1992; Dolcos et al., 2005; Weymar et al., 2011) retention intervals. Moreover, interacting effects of emotion and memory were revealed in our study, but when considering global topographical changes and their estimated generators in the inverse solution space.

The use of high-density EEG further allowed us to gain insight into the putative brain networks giving rise to proactive processes during scene recognition. Four hundred ms after stimulus onset, we found that the topography of the evoked electric field reliably changed depending on the amount of perceptual evidence accumulated, unambiguously revealing changes in the configuration of the underlying brain networks (Lehmann and Skrandies, 1980; Michel and Murray, 2012; Michel et al., 1999; Pourtois et al., 2008). Moreover, these topographical effects were different for old vs. new scenes. Two images before recognition, we found that the dominant occipital positivity/frontal negativity topographical map was decreased for old compared to new scenes, and this memory effect later influenced the concurrent occipital positivity/frontal positivity scalp map. These topographies are thought to reflect memory-related processes that are shaped both by the amount of perceptual evidence accumulated at a given moment in time, as well by specific top-down mechanisms, including affective processes (as suggested by the activity pattern of the estimated neural sources). These results suggest that memory could rapidly alter the expression of accumulation of evidence processes taking place prior to overt recognition, probably via the activation of non-overlapping brain structures during the processing of old vs. new scenes (Ranganath and Rainer, 2003). By contrast, the temporal dynamic of these two dominant topographical maps was not reliably influenced by the emotional content of the scenes, replicating our previous results (Schettino et al., 2011).

Modulatory effect of emotion depends on memory

In agreement with the assumption of non-overlapping brain networks between new and old scenes, our complementary source localization analysis confirmed that the processing of old scenes was mostly achieved by a distributed network of ventral brains regions, including the PHG and FG, whereas the processing of new scenes involved mainly neural changes in more dorsal brain regions at the same latency, including the dACC and the insula. Interestingly, we found that activity extracted in these ROIs was influenced by the emotional content of the scenes, though at different stages during the accumulation of evidence depending on the actual memory status of these scenes. These results suggest that emotion may exert pervasive effects on these proactive processes during scene recognition. Accordingly, the estimation of the neural sources of the ERP signal using a linear distributed inverse space turned out to be more sensitive to capture subtle changes related to the processing of the emotional content of the scenes, compared to the topographical mapping analyses carried out using 128 channels (Esslen et al., 2004; Pascual-Marqui et al., 2002). This dissociation is

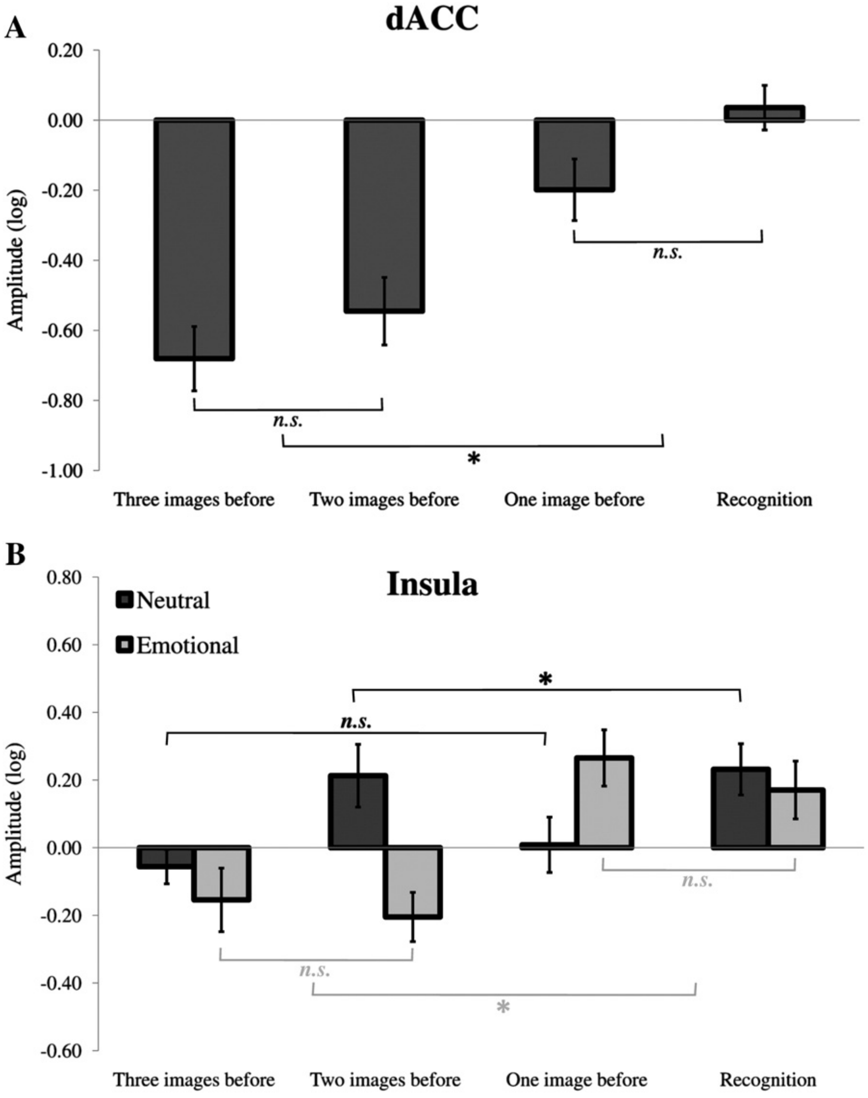

Fig. 6. (A) Estimated current density values for the dACC (new scenes) as a function of recognition level. A categorical increase in activity was observed between two images and one image before recognition. (B) Activity in the insula for new scenes, separately for neutral and emotional pictures, as a function of time of recognition. A stable pattern of activity was evidenced in the insula in response to neutral pictures, confirmed by a lack of statistically significant differences among all four recognition levels, except between three image before and recognition. By contrast, insula activity sharply increased between two images and one image before recognition for emotional scenes. (C) and (D) Estimated current density values for the PHG (C) and the FG (D) (old scenes). A monotonic increase of activity in these regions as a function of accumulation of perceptual evidence was observed. Moreover, higher activity for neutral (dark gray bars) vs. emotional (light gray bars) scenes was found three images before recognition. * $p < .05$; ** $p < .01$; *** $p < .001$. Vertical bars correspond to standard errors of the mean.

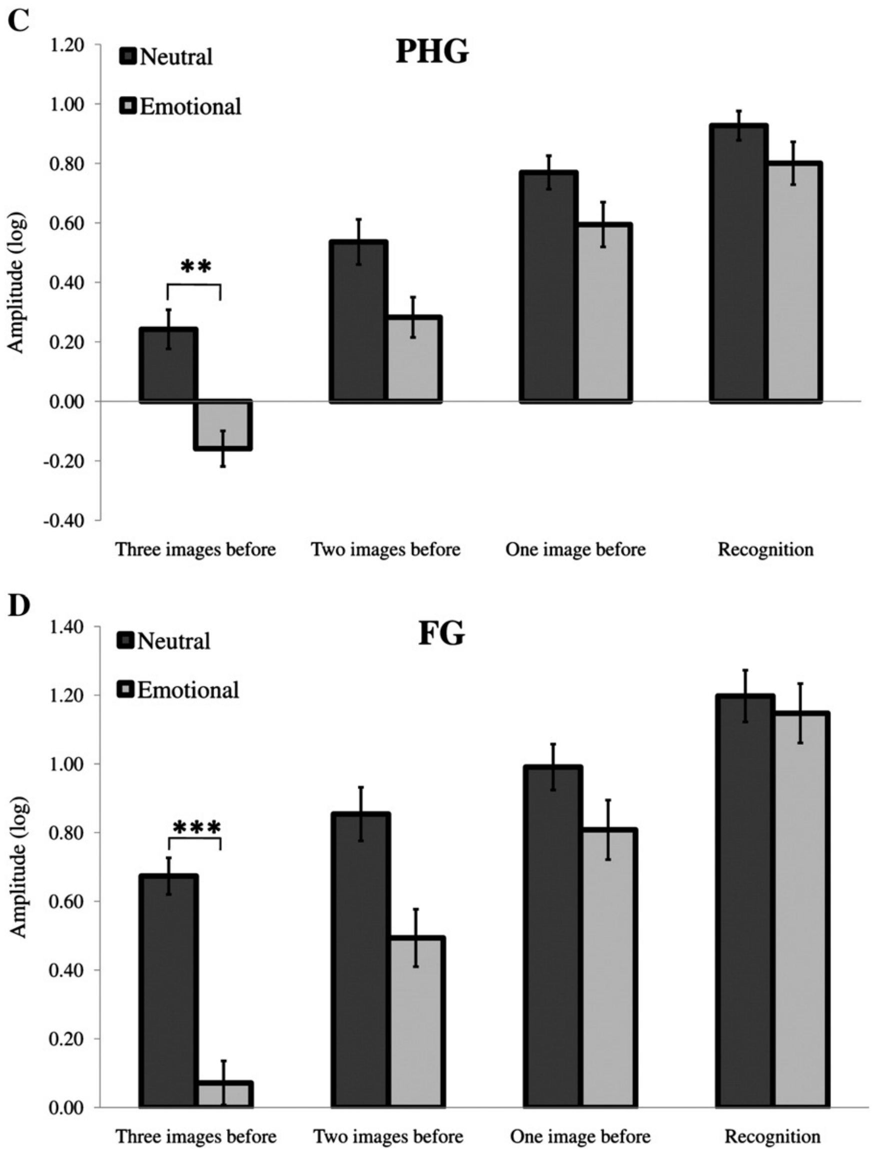

Fig. 6 (*continued*).

not surprising though, given the enhanced spatial sensitivity of distributed source localization methods (including sLORETA) that enables to reveal subtle differences between experimental conditions, which may be otherwise difficult to capture based on local amplitude measurements performed at the sensor level (Brodbeck et al., 2011; Lantz et al., 2001; Michel and Murray, 2012).

Enhanced uncertainty during the processing of new scenes

Activity in the dACC for neutral scenes was low and close to baseline until one image before recognition, when a sharp increase took place (see Fig. 6A). This specific response profile for the dACC, which is consistent with the involvement of this medial frontal region in higher-order decision making processes (Bush et al., 2002; Ridderinkhof et al., 2004; Seo and Lee, 2007), was already found in previous imaging studies looking at accumulation of evidence processes taking place during object or scene recognition (Ploran et al., 2007, 2011; Wheeler et al., 2008). This sharp increase in the dACC close to recognition could reflect either uncertainty or conflict, given the urge to stop the stimulus sequence and take a decision before the sequence comes to an end, while the accumulated sensory evidence may not be completed yet (Anderson et al., 2009; Philiastides and Sajda, 2007; Sohn et al., 2007). Interestingly, a similar effect in the dACC was already reported in our previous ERP study, though based on a different task (Schettino et al., 2011). Hence, this region may be involved in the coding of conflict or uncertainty during perceptual decision making tasks at a more general level (Ridderinkhof et al., 2004; Ullsperger et al., 2004), particularly when recognition targets are embedded in an emotional context (Kanske and Kotz, 2011a, 2011b).

Not only the dACC, but also the insula showed increased activity in response to new scenes, although it additionally showed a modulation according to the emotional content of the scenes (Fig. 6B). Activation of the insula has previously been reported for a variety of tasks and stimuli (Craig, 2009), including when exogenous sensory stimuli acquire salience (Seeley et al., 2007), as well as in response to challenging and uncertain perceptual tasks (Grinband et al., 2006; Philiastides and Sajda, 2007). Likewise, previous ERP work based on a similar approach as used here already source-localized the insula during the early processing of response errors during a speeded go/no-go task (Dhar et al., 2011). Presumably, similar effects could explain the involvement of the insula in our task during the accumulation of perceptual evidence prior to recognition. Whereas uncertainty likely decreased as a function of accumulation of evidence, at time of recognition this process is perhaps not completed yet. Noteworthy, emotional stimuli could somehow exacerbate this process in the insula, thereby shifting the neural response earlier in time – probably because of their intrinsic motivational salience – compared to neutral stimuli. Presumably, the emotional content of the stimulus might actively interfere with task demands (memory matching task), resulting in an earlier experience of uncertainty or conflict for emotional compared to neutral scenes.

More generally, the parallel involvement of the insula and dACC in our study during the processing of new scenes is not surprising, but consistent with many previous findings showing that these two regions likely operate together and eventually form a functional network activated across a variety of stimuli and tasks (Ploran et al., 2007; Seeley et al., 2007; Sterzer and Kleinschmidt, 2010), including the implementation of task sets (Dosenbach et al., 2008; Nelson et al., 2010), awareness processes (Craig, 2009; Dhar et al., 2011; Mayr, 2004), as well as performance monitoring (Ito et al., 2003; Ridderinkhof et al., 2004; Wheeler et al., 2008).

Emotion-dependent monotonic accumulation of perceptual evidence in ventral object-selective regions during the processing of old scenes

While the processing of new scenes was selectively associated with specific neural effects in the dACC and insula starting ~400 ms post-stimulus onset, a different picture emerged for the processing of old scenes at the same latency, where ventral object-sensitive brain regions were found to be significantly more active. Among them, activity in the PHG increased linearly as a function of accumulation of evidence, with the lowest amplitude values three images before recognition and the highest at time of recognition (see Fig. 6C). Given the ubiquitous involvement of this specific brain area in the processing of contextual information needed for successful scene recognition (Bar and Aminoff, 2003; Bar et al., 2008; Kveraga et al., 2011), we interpreted our new results as reflecting similar mechanisms. The linear trend found in this region during accumulation of evidence prior to recognition (see also Schettino et al., 2011) is consistent with the assumption that this region is rapidly involved in the analysis of diagnostic contextual information, primarily conveyed by magnocellular input (Bar, 2004, 2007, 2009). Interestingly, we found that this response profile was not identical for emotional compared to neutral scenes. More specifically, during early stages of accumulation of evidence (i.e., three images before recognition), the amplitude of the PHG was significantly lower for emotional compared to neutral scenes. An early interference effect probably took place for emotional scenes, eventually preventing the initiation of the generative accumulation of evidence process (presumably based on contextual information carried by LSF cues) taking place in this region. However, because at time of recognition this amplitude difference between neutral and emotional scenes was no longer significant, it is likely that a more rapid accumulation of evidence took place in this region for emotional compared to neutral scenes. Hence, emotional factors would initially interfere with the processing of diagnostic contextual information (based on the extraction of LSF cues), but later boost this same process when more evidence is timely gathered and accumulated (Fig. 6C), presumably based on the concurrent processing of HSF information. Such an interpretation is compatible with mounting evidence showing the importance of contextual visual information during emotional scene recognition (Barrett and Kensinger, 2010; Barrett et al., 2011; de Gelder et al., 2006; Righart and De Gelder, 2006, 2008a, 2008b). Thus, due to their enhanced motivational relevance, emotional scenes led to a steeper accumulation of evidence in the PHG relative to neutral scenes.

A comparable outcome was found for the FG (Fig. 6D). Previous imaging studies already reported the involvement of the FG in the gradual accumulation of perceptual evidence (James et al., 2000; Malach et al., 1995). Presumably, a similar accumulation of evidence mechanism took place in the FG in our study, although one may argue that the diagnostic visual information used by this region may be different compared to the PHG. More specifically, the FG could be involved in the accumulation of perceptual evidence based on the rapid extraction of invariant object features or viewpoint information, as opposed to contextual information in the PHG (Epstein et al., 1999; Grill-Spector and Malach, 2004; Malach et al., 1995; Pourtois et al., 2005, 2010).

Although all these effects were obtained for female participants only, we surmise that similar results could be obtained in male participants, given the specifics of our procedure and stimulus selection. In fact, the IAPS pictures used in our study did not include highly arousing pictures (e.g., mutilations or erotica), for which gender differences might likely arise (Lithari et al., 2010; Proverbio et al., 2009; Schupp et al., 2006, 2007). Moreover, future studies are needed to assess whether the reported ERP effects may lead to differential long-term memory effects for emotional compared to neutral scenes (Dolcos and Cabeza, 2002; Kaestner and Polich, 2011).

Conclusion

The results of this study shed light on the electrophysiological correlates (and the estimated brain sources) of accumulation of perceptual evidence prior to scene recognition. Four hundred ms following stimulus onset, regions in the dACC and insula were selectively active prior to overt recognition of new scenes, likely translating either enhanced uncertainty or conflict monitoring during perceptual decision making. Interestingly, activity in the insula was elicited earlier for emotional compared to neutral scenes, suggesting prioritized processing for this class of stimuli due to their enhanced motivational salience, particularly in perceptually ambiguous tasks. By contrast, at the same latency following stimulus onset, old scenes recruited primarily ventral object-selective regions during accumulation of perceptual evidence, including the PHG and FG. Interestingly, an early modulation of their response profile as a function of the emotional content of the scenes was observed. Accordingly, even though neural mechanisms underlying accumulation of evidence during scene recognition are multiple and can be dissociated based on memory (i.e., old vs. new scenes), it is striking to observe that emotion exerts pervasive interference effects on these proactive processes during fairly early stages of accumulation of perceptual evidence (when the retinal input is still minimal or impoverished). Our new ERP findings are consistent with a recent theoretical proposal (Barrett and Bar, 2009) suggesting that the affective properties of the visual input are intrinsically embedded in the predictions generated during the rapid extraction of its gist. Given the direct anatomical projections from specific medial frontal brain areas (including the ACC and insula) – active during recognition processes – to autonomic and endocrine output centers in the hypothalamus, midbrain, and brainstem, internal affective states of the organism might potentially be one feature of the set of predictions used to facilitate recognition (Bar, 2004; Bar and Aminoff, 2003; Barrett and Bar, 2009).

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Conflict of interest

The authors declare that there is no conflict of interest.

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