

1 Running head: EFFECTS OF EMOTION AND MEMORY ON SCENE RECOGNITION

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

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Abstract

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

41 **Keywords:** scene recognition, emotion, high density ERP, sLORETA, parahippocampal gyrus,
42 fusiform gyrus, dorsal anterior cingulate cortex, insula.

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

45 **1. Introduction**

46 Visual scene recognition results from dynamic and reciprocal interactions between bottom-up
47 sensory processing and top-down modulatory influences, including selective attention (Treisman
48 and Kanwisher, 1998), contextual information (Oliva and Torralba, 2007), and prior expectations
49 (Summerfield and Egner, 2009). Interestingly, it has been proposed that the differential sensory
50 processing of low (LSF) and high (HSF) spatial frequency information could underlie reciprocal
51 interaction effects between bottom-up sensory processing and top-down expectations (Bar, 2007,
52 2004, 2003). In this framework, the rapid extraction of LSF information via dedicated
53 magnocellular pathways may serve to quickly generate coarse predictions regarding the most
54 probable content of the visual scene. This process would later be assisted and refined by the
55 extraction of HSF information.

56 Whether these dynamic perceptual processes are differentially engaged depending on the
57 (perceived) emotional content of the scenes, however, has received little attention so far.
58 Mounting evidence shows that emotion exerts strong biases on visual perception (Öhman et al.,
59 2001; Pourtois et al., 2012; Todd et al., 2012; Vuilleumier, 2005), including at early stages of
60 recognition (Damaraju et al., 2009; Halgren et al., 2000; Pourtois et al., 2004). Thus, emotion is
61 no longer seen as a byproduct of perception but, instead, as a core determinant of it (Pourtois et
62 al., 2012). Accordingly, proactive processes during scene recognition are unlikely to be immune
63 to emotion, defined here as the acquired valence and arousal values of the stimulus (Barrett et al.,
64 2007; Lang, 1995; Russell, 1980). More specifically, the speed and extent of iterative processes
65 between bottom-up processing and top-down expectations during scene recognition are probably

66 subject to variations depending on the rapidly extracted emotional meaning of the stimulus.
67 Consistent with this assumption, we recently reported evidence for the modulation of scene
68 recognition processes by emotion (Schettino et al., 2011). In this study, participants were
69 presented with series of pictures whose content was progressively revealed by increasing, in up
70 to six sequential steps, the amount of LSF and HSF information. This *progressive unfolding task*
71 was used to mimic a “coarse-to-fine” decomposition of the retinal input, presumably fostering
72 the online generation of guesses regarding the most likely identity of the stimulus (Bar, 2003;
73 Bullier, 2001; Hegdé, 2008). Participants were asked to discriminate the content of the stimulus
74 progressively revealed by performing an orthogonal animacy judgment task. Crucially, the
75 scenes used in this experiment were neutral, pleasant, or unpleasant. Behavioral results showed a
76 delayed recognition for emotional compared to neutral scenes. At the electrophysiological level,
77 we found reliable ERP differences starting at approximately 280 ms after stimulus onset,
78 depending on the amount of perceptual evidence accumulated. Estimated activity in the posterior
79 cingulate cortex (PCC) and the parahippocampal gyrus (PHG) showed a response profile
80 characterized by a linear and monotonic accumulation of perceptual evidence. Conversely,
81 categorical recognition effects were evidenced in medial frontal regions, including the dorsal
82 anterior cingulate cortex (dACC). However, none of these brain effects, albeit consistent with
83 previous neuroimaging results (Carlson et al., 2006; James et al., 2000; Ploran et al., 2011,
84 2007), was found to be influenced by the emotional content of the scenes.

85 This lack of modulatory effect of emotion on these brain mechanisms was imputed to two
86 main factors. First, it was hypothesized that the elected procedure did not effectively promote the
87 generation of unambiguous predictions regarding the likely identity of the scenes progressively
88 revealed, since participants were mainly presented with visually impoverished versions of

89 pictures that they had never encountered before. Second, the use of an orthogonal animacy
90 judgment task might have strongly reduced the salience of the emotional features of the scenes.
91 Several studies showed that (early and automatic) affective stimulus processing is substantially
92 reduced when concurrent, non-affective semantic stimulus dimensions become task-relevant
93 (Everaert et al., 2011; Pessoa, 2008; Pessoa et al., 2002; Spruyt et al., 2007). To overcome these
94 limitations, we devised a modified version of the progressive unfolding task (Schettino et al.,
95 2012). In this latter study, to promote the generation and use of a restricted number of predictions
96 regarding the identity of the scenes progressively revealed, we introduced a standard delayed
97 match-to-sample manipulation (Courtney et al., 1997; Goldman-Rakic, 1990; Henson et al.,
98 2005; Rugg et al., 1998). On each trial, participants were first asked to encode a complex
99 colorful scene having either a neutral or emotional meaning. After a constant time interval, the
100 content of either the same or a novel scene was progressively revealed (similarly to Schettino et
101 al., 2011), and participants were asked to perform a delayed match-to-sample task. In addition,
102 we occasionally asked participants to rate the emotional content of the scenes (besides the
103 delayed match-to-sample task), thereby ensuring that the emotion features were directly attended
104 throughout the whole experimental session. Behavioral results revealed earlier recognition for
105 old compared to new scenes in all emotion conditions, providing evidence that participants used
106 restricted (short-term) memory representations to perform the task. Notably, delayed recognition
107 was observed for emotional relative to neutral scenes, replicating our previous behavioral results
108 (Schettino et al., 2011).

109 The present paper reports the electrophysiological results of the aforementioned behavioral
110 study (Schettino et al., 2012). Our main objective was to compare, using advanced EEG
111 methods, the processing of previously encountered (“old”) vs. “new” scenes, in order to evaluate

112 whether any influence of emotion on brain mechanisms underlying scene recognition was
113 depending on the (short-term) memory status of these complex visual stimuli. To verify that our
114 short-term memory manipulation was effective, we analyzed a distinctive ERP signature of
115 recollection processes, a late positive ERP waveform typically recorded from centro-parietal
116 sites starting at approximately 500 ms post-stimulus onset (Curran and Cleary, 2003; Curran and
117 Doyle, 2011; Rugg and Curran, 2007; Voss and Paller, 2006). Based on previous literature, we
118 expected to observe more positive ERPs after correctly recognized old pictures compared to
119 correctly classified new pictures, the so-called ‘old/new effect’ (Rugg and Curran, 2007; Voss
120 and Paller, 2008; Wilding et al., 1995). Topographic analysis and complementary source
121 localization methods were subsequently employed to investigate whether dissociable response
122 profiles could be evidenced as a function of memory status and emotional valence of the scenes.
123 Similarly to our previous study (Schettino et al., 2011), reliable topographical differences were
124 expected to be observed in a time window following the low-level visual discrimination of the
125 stimulus (i.e., after the N1 and P2 ERP components). In addition, we used a standard distributed
126 source localization method to estimate the configuration of the neural generators of the main
127 topographical maps identified by the preceding analysis. We assessed whether differential
128 activation profiles in specific ventral brain areas as opposed to dorsal/medial frontal regions
129 might be found, reflecting accumulation of evidence and decision-related processes, respectively.

130 2. **Methods**

131 2.1. *Participants*

132 Twenty-two undergraduate psychology students (all women, mean age 21 years, range 18-26)
133 participated in the study, which was approved by the local Ethics Committee. All participants
134 were native Dutch speaking, right-handed, had normal or corrected-to-normal vision, with no

135 history of neurological or psychiatric disorders. The data of one participant could not be saved
136 properly because of technical problems, whereas the EEG data of three other participants were
137 discarded due to excessive artifacts and a low signal-to-noise ratio. Thus, the final sample
138 consisted of 18 participants. All volunteers gave informed written consent prior to their
139 participation, and were compensated 30€.

140 2.2. *Stimuli*

141 The visual stimuli were selected from the International Affective Picture System (IAPS; Lang
142 et al., 2008). Three-hundred and sixty pictures were pre-selected, equally divided into three
143 emotion categories according to their pre-defined valence scores: *neutral*, *unpleasant*, and
144 *pleasant* (see Table 1 in Schettino et al., 2012). Of note, these pictures were selected on the basis
145 of mean valence and arousal ratings reported by female responders (Lang et al., 2008), because
146 only women eventually participated in the experiment (see above). Similar to Schettino et al.
147 (2011), we selected scenes that were neither highly pleasant (i.e., erotic situations) nor highly
148 unpleasant (i.e., mutilations), because these categories were associated with specific emotion
149 reactions in previous research (Schupp et al., 2006, 2007). We also included 16 additional neutral
150 pictures that were only used during the practice session (not included in the subsequent statistical
151 analyses). Furthermore, 36 supplementary neutral scenes were scrambled (i.e., each scene was
152 divided into arbitrary grids of 255x255 pixels, whose locations were randomly shuffled 10 times)
153 and, as a result, their content was made meaningless. Thus, in total, participants were presented
154 with 412 IAPS scenes¹.

155 The selected IAPS pictures were resized to 922 x 691 pixels (90% of the original 1024 x 768
156 pixel size), and they were presented at the beginning of each trial (see details below). For the
157 progressive unfolding procedure, a separate pre-processing was carried out on the original IAPS

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

158 scenes (1024 x 768 pixels) (Schettino et al., 2011). First, a grayscale conversion was applied
159 using the algorithm included in Adobe Photoshop 6.0 (Adobe Systems, Mountain View, CA).
160 Afterwards, six bandpass spatial frequency filters were applied on each and every picture using
161 the fast Fourier transform (FFT) included in ImageJ v1.44 (<http://rsb.info.nih.gov/ij/>; for a
162 similar procedure, see Delplanque et al., 2007). As a result, six distinct levels of filtering were
163 obtained for every IAPS scene, each containing a different amount of low and high spatial
164 frequency information². All these modified pictures were finally resized to 768 x 576 pixels
165 (75% of the original IAPS pictures). Importantly, the grayscale and resize picture conversions
166 relative to the colorful picture were performed to discourage participants to use a purely
167 perceptual, pixel-to-pixel matching strategy to retrieve the content of the initial picture during the
168 memory matching task (see *Procedure* below).

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

179 2.3. Procedure

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).

180 Participants were individually tested in a small, dimly lit room, and seated at a viewing
181 distance of 75 cm in front of a 19" CRT computer screen (refresh rate: 100 Hz). After filling out
182 the informed consent, they were presented with task instructions, followed by a practice block
183 containing 16 trials (with neutral pictures). Then, they moved on to the main experimental
184 session, which was divided into twelve blocks (separated by short breaks), each containing 33
185 trials (Schettino et al., 2012; see also Fig. 1A). Each trial began with a 1500ms presentation of a
186 colorful, fully detailed picture subtending $18.5^\circ \times 13.9^\circ$ of visual angle, followed by a 2000ms
187 grayscale mask. At the offset of the mask, the unfolding sequence started. A fixation cross
188 appeared in the center of the screen for 250 ms. The first grayscale, blurred image level of a
189 given picture (subtending $15.4^\circ \times 11.6^\circ$ of visual angle) was then presented for 500 ms, followed
190 by a 250ms blank screen. Next, the second image level of the same picture (containing slightly
191 more HSF and LSF information) was displayed for 500 ms, plus the 250ms blank screen, and the
192 same procedure was repeated until the presentation of the sixth, non-filtered image level. The
193 inter-trial interval was set at 1000 ms. Participants were required to provide two separate and
194 consecutive manual responses (see also Schettino et al., 2011, for a similar dual response
195 procedure). First, they were asked to press, with their right index finger, a pre-defined button on
196 a response box (Cedrus RB-730; <http://www.cedrus.com/responsepads/rb730.htm>) as soon as
197 they gathered enough perceptual evidence to decide whether the content of the unfolded scene
198 was either the same as the one displayed during the encoding phase, a new one, or a scrambled
199 picture (Response1)³. Pressing the button immediately interrupted the presentation of the
200 stimulus sequence. Although instructions emphasized accuracy, participants were encouraged to
201 stop the sequence as soon as they felt they could recognize the content of the scene, which

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.

202 occurred before the end of the sequence for a vast majority of trials (see Schettino et al., 2012).
203 After 500 ms, participants were required to validate their Response1 by pressing, on a standard
204 AZERTY keyboard, the “o” key if the unfolded scene was the same as the colorful one
205 previously presented (“old” condition), the “n” key if these two scenes were different (“new”
206 condition), or the “s” key if the unfolded scene was displaying a meaningless content
207 (“scrambled” condition). All these responses, for which no time limit was imposed, were coded
208 as Response2. This dual response procedure was used for three main reasons: (i) to dissociate
209 early visual recognition effects (Response1) from the overt discrimination and comparison in
210 short-term memory of the scenes (Response2); (ii) to remove recognition errors (based on
211 accuracy of Response2) from the behavioral and ERP analyses; (iii) to minimize the potential
212 contamination of ERP data by the activation of competing motor responses across the three
213 different conditions, since Response1 always required to press a single button shared across
214 conditions. To further prevent the use of a recognition strategy solely based on low-level visual
215 features, the content of half of the “old” scenes was unpredictably flipped along the horizontal
216 axis between encoding and retrieval. Participants were informed that an “old” response was to be
217 given for these “flipped” trials, since the memory matching task had to be performed primarily
218 based on the *content* of the scenes. For the statistical analyses of the behavioral and EEG data
219 reported hereafter, “old flipped” and “old unflipped” trials were combined into a single “old”
220 condition, and these “old” trials were eventually compared to “new” trials (see also Schettino et
221 al., 2012). Hence, using this procedure, for each emotion category (neutral, pleasant, unpleasant),
222 two trial types were compared to each other: “old”, in which the identity of the colorful picture
223 was identical to the scene progressively unfolded; “new”, meaning that the identities of the
224 colorful and unfolded scene were different (although matched as far as possible in terms of low-

225 level visual properties). Importantly, for “new” scenes, no change in terms of emotional content
226 ever occurred between the colorful picture and the gradually unfolded scene. In other words, a
227 neutral colorful picture was always followed by the unfolding of a neutral scene, and the same
228 occurred for emotion-laden stimuli (pleasant-pleasant; unpleasant-unpleasant; see Table 2 in
229 Schettino et al., 2012).

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

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

242 2.4. *Recording and pre-processing of EEG data*

243 Electroencephalographic (EEG) activity was continuously recorded using a BIOSEMI Active-
244 Two system (BioSemi, Inc., The Netherlands; <http://www.biosemi.com>) by means of 128
245 Ag/AgCl electrodes fitted into a stretching cap and following the BioSemi ABCD position
246 system (i.e., electrode positions are radially equidistant from CZ;
247 <http://www.biosemi.com/headcap.htm>). Two additional electrodes, the common mode sense

248 (CMS) active electrode and the driven right leg (DRL) passive electrode, were used as reference
249 and ground electrodes, respectively (http://www.biosemi/faq/cms_and_drl.htm). Vertical electro-
250 oculograms (vEOG) were monitored using two additional electrodes placed on the inferior and
251 superior areas of the left orbit, whereas horizontal EOG (hEOG) were recorded by means of two
252 electrodes situated symmetrically on the outer canthus of each eye. EEG and EOG recordings
253 were sampled at 512 Hz.

254 ERPs of interest were computed offline using Brain Vision Analyzer 2.0 (Brain Products™
255 GmbH, Munich, Germany; www.brainproducts.com). First, a topographic interpolation
256 (interpolation by spherical splines; Perrin et al., 1989) was applied on noisy channels
257 (interpolated channels across 18 subjects: $M = 3.78$, $SD = 4.28$, range 0-11), and a common
258 average reference was then applied. Afterwards, the continuous EEG signal was segmented into
259 individual epochs, excluding trials corresponding to errors (based on accuracy on Response2).
260 Similar to our previous study (Schettino et al., 2011), four main epochs were computed around
261 stimulus onset (using an interval of 200 ms prior to and 750 ms after this event), enabling us to
262 look backwards at visual ERPs progressively elicited prior to Response1: (1) segments in which
263 Response1 occurred from 0 to 750 ms after stimulus presentation (“recognition”); (2) segments
264 in which Response1 occurred from 750 to 1500 ms after stimulus presentation (“one image
265 before” recognition); (3) segments in which Response1 occurred from 1500 to 2250 ms after
266 stimulus presentation (“two images before” recognition); (4) segments in which Response1
267 occurred from 2250 to 3000 ms after stimulus presentation (“three images before” recognition).
268 A segment length of 750 ms was used in order to include stimulus presentation duration (500 ms)
269 as well as the following 250ms blank screen. These parameters minimized the possibility that
270 late ERPs for the preceding image level could substantially contaminate the pre-stimulus

271 baseline of the current image level (see Figs 3 and 4A). All these individual segments were then
272 baseline corrected using the entire pre-stimulus interval of 200 ms, before a standard ocular
273 correction was performed (Gratton et al., 1983). Artifact rejection was then carried out
274 ($-80/+80\mu\text{V}$ amplitude scale across participants) to remove segments contaminated by artifacts,
275 including residual eye blinks and muscle activity. Finally, stimulus-locked ERP averages were
276 computed, separately for each condition (memory: 2 levels; emotion: 3 levels; recognition times:
277 4 levels), resulting in 24 individual ERP averages. However, because no difference in recognition
278 between unpleasant and pleasant pictures was observed at the behavioral level (see also
279 Schettino et al., 2012), these two emotion conditions were collapsed in order to increase the
280 signal-to-noise ratio, leaving a total number of 16 individual ERP averages (percentage of
281 segments kept after pre-processing: $\sim 79\%$)⁴. These averages were eventually low-pass filtered
282 using a 30 Hz cutoff (slope 12dB/oct).

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

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; (16) old, three images before, emotional: $M = 84$, range 67-105.

290 2.5. *Analysis of ERP data*

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

296 Second, to investigate the classical old/new effect (Rugg and Curran, 2007; Voss and Paller,
297 2008; Wilding et al., 1995), we analyzed the average amplitude of the centro-parietal ERP
298 component (recorded from electrode A19, which corresponds to Pz in the 10/20 international
299 EEG system) time-locked to the time of recognition, extracted from a 500-750ms time window
300 post-stimulus onset (Paller et al., 2003; Voss and Paller, 2006)⁵. Paired-samples t-tests were used
301 to verify a mean amplitude difference of this late positive potential between old and new scenes.

302 To examine the ERP data recorded during the progressive unfolding sequence, reference-free
303 topographic analyses were used, similarly to our previous study (Schettino et al., 2011). This
304 method allows to summarize a complex ERP data set into a smaller number of dominant scalp
305 topographies (i.e., global configuration of the electric field across all 128 channels at each time
306 frame) (Lehmann and Skrandies, 1980; Michel and Murray, 2012; Michel et al., 2001, 1999;
307 Murray et al., 2008; Pourtois et al., 2008). These analyses enable to assess how the distribution
308 and expression of these dominant topographies vary in time across experimental conditions,
309 irrespective of changes in the strength of the ERP signal. Topographic analyses were performed
310 using CARTOOL software (version 3.43; <http://brainmapping.unige.ch/Cartool.htm>; see also

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.

311 Brunet et al., 2011). The dominant scalp maps were identified in the grand-average ERP data for
312 each main condition (recognition, one image before, two images before, and three images before)
313 over a wide time window spanning from 0 to 600 ms after stimulus onset. To this end, a specific
314 spatiotemporal clustering algorithm, the “Atomize and Agglomerate Hierarchical Clustering”
315 (AAHC; for a detailed description, see Murray et al., 2008; Tibshirani and Walther, 2005), was
316 used. The optimal number of dominant maps best “explaining” the ERP dataset was determined,
317 following standard practice, using a cross-validation criterion (Pascual-Marqui et al., 1995).
318 Next, the spatial correlation between single-subject ERPs and the aforementioned template maps
319 identified by the AAHC clustering algorithm was calculated (a procedure called “fitting”;
320 Brandeis et al., 1995; Murray et al., 2008), in order to obtain a quantitative estimate of each
321 map’s relative expression across subjects and conditions, as defined by the Global Explained
322 Variance (GEV, or goodness of fit). GEV values were entered in repeated measures ANOVAs,
323 with recognition level, memory, and emotion as within-subject factors. Paired t-tests were used
324 as post-hoc comparisons between conditions, when required to back up significant interaction
325 effects. Whenever Mauchly’s test indicated that the assumption of sphericity had been violated,
326 the degrees of freedom were corrected using Greenhouse-Geisser estimates. The alpha level was
327 set at $p < 0.05$.

328 2.6. *Source localization analysis*

329 To estimate the putative neural generators underlying the dominant voltage topographies
330 identified at the scalp level by the previous analyses, we used sLORETA (Pascual-Marqui,
331 2002). sLORETA is a distributed linear inverse solution based on the neurophysiological
332 assumption of coherent co-activation of neighboring cortical areas, known to have highly
333 synchronized activity (Silva et al., 1991). Accordingly, it estimates multiple simultaneously

334 active sources without any *a priori* assumption on the number and position of the underlying
335 dipoles (for a mathematical validation of this localization technique, see Sekihara et al., 2005).
336 sLORETA solutions are computed within a three-shell spherical head model co-registered to the
337 MNI152 template (Mazziotta et al., 2001), restricted to the gray matter and the hippocampus.
338 The source locations were therefore given as (x, y, z) coordinates (x from left to right; y from
339 posterior to anterior; z from inferior to superior). The estimation of the three-dimensional
340 intracerebral current density distribution is performed in 6239 voxels, each containing an
341 equivalent current dipole. The head model for the inverse solution uses the electric potential lead
342 field computed with a boundary element method applied to the MNI152 template (Fuchs et al.,
343 2002). Scalp electrode coordinates on the MNI brain are derived from the international 5%
344 system (Jurcak et al., 2007). The calculation of all reconstruction parameters was based on the
345 computed common average reference.

346 sLORETA units were scaled to amperes per square meter (A/m^2), normalized across subjects,
347 and nonparametric statistics were then applied on log-transformed data. Direct statistical
348 comparisons between conditions were performed in this inverse solution space using repeated
349 measures ANOVAs and post-hoc paired t-tests. The level of significance for all these analyses
350 was set at $p < 0.05$.

351 3. Results

352 3.1. Emotion classification task

353 Results of the emotion classification task showed high (i.e., more pleasant) ratings for
354 pleasant ($M = 6.14$, $SD = 0.81$) scenes, followed by neutral ($M = 4.89$, $SD = 0.58$) and unpleasant
355 ($M = 3.45$, $SD = 1.06$) scenes. A one-way ANOVA performed on these mean ratings disclosed a
356 highly significant effect of emotion [$F(2, 34) = 39.94$, $p < .001$, $\eta_p^2 = .701$]. Paired samples t-

357 tests carried out on these mean ratings confirmed highly significant differences between neutral
358 and unpleasant pictures [$t(17) = 4.83, p < .001$], as well as between neutral and pleasant [$t(17) =$
359 $-7.47, p < .001$] and unpleasant and pleasant [$t(17) = -6.81, p < .001$] scenes. Thus, participants
360 rated the emotional valence of the pre-selected stimuli in accordance with the published
361 normative scores (Lang et al., 2008). These results also confirmed that participants correctly
362 attended to the actual emotional content of the scenes throughout the experiment.

363 3.2. Accuracy for the progressive unfolding task

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

373 3.3. LPP during stimulus encoding

374 Fig. 2 shows the grand-average ERPs recorded from an array of medial centro-parietal
375 electrode sites (A8, A20, B5). These electrodes were selected for illustration purposes after an
376 initial 2 (emotion) x 9 (electrode) repeated measures ANOVA revealed no significant interaction
377 effect between these two factors ($p > .05$). The analysis performed on the mean amplitude of the
378 LPP showed a larger sustained positive component for emotional ($M = 5.86 \mu\text{V}, SD = 4.32$)
379 relative to neutral ($M = 4.91 \mu\text{V}, SD = 4.47$) scenes. Paired t-tests confirmed a significant

380 amplitude difference between neutral and emotional scenes [$t(17) = -3.75, p = .002$]. Thus, these
381 results provided additional evidence for the differential processing of the emotional content of
382 the scenes encoded in short-term visual memory prior to unfolding. We also performed
383 correlation analyses between the LPP amplitude and task performance (i.e., memory accuracy
384 during the progressive unfolding task), separately for new, old, neutral, and emotional scenes.
385 However, no significant correlation was observed (all $ps > .05$).

386 3.4. *Old/new ERP effects at time of recognition*

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

395 3.5. *Topographic analysis of ERPs recorded during the unfolding task*

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

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.

402 characterization of this topographical change starting ~400 ms following stimulus onset is
403 provided.

404 At the offset of the P2 scalp map, for three, two, and one image before recognition, an
405 occipital positivity with a concurrent, broad frontal negativity was evidenced. Conversely, an
406 occipital positivity accompanied by a more focal frontal positivity was observed one image
407 before recognition, being then predominant at time of recognition (Fig. 4B). These two
408 distinctive dominant topographical components were then fitted back to the individual ERP data.
409 Based on the outcome of the spatiotemporal analysis, we selected a large time interval lasting
410 120 ms, namely from 402 to 522 ms after stimulus onset, during which these topographic
411 differences were most obvious (Fig. 4B). A 2 (map configuration: occipital positivity/frontal
412 negativity, occipital positivity/frontal positivity) x 4 (recognition level: recognition, one image
413 before, two images before, three images before) repeated measures ANOVA on the GEV values
414 obtained for these two specific topographies after fitting revealed significant main effects of map
415 configuration [$F(1, 17) = 7.40, p = .015, \eta_p^2 = .303$] and recognition level [$F(3, 51) = 10.69, p <$
416 $.001, \eta_p^2 = .386$], as well as a highly significant η_p^2 map configuration x image level interaction [$F(3,$
417 $51) = 9.53, p < .001, \eta_p^2 = .359$]. Interestingly, pairwise comparisons showed that the GEV of the
418 occipital positivity/frontal positivity map progressively increased from three images before
419 recognition to actual recognition (all $ps < .05$, except two images vs. three images before
420 recognition, $p = .079$) (see Fig. 4D). By comparison, the GEV of the occipital positivity/frontal
421 negativity showed a different pattern (Fig. 4C). Paired t-tests revealed a sharp increase in GEV
422 from three to two images before recognition [$t(17) = -3.88, p = .001$], followed by a gradual
423 decrease between two images before and time of recognition [$t(17) = 3.21, p = .005$], as well as
424 between one image before and actual recognition [$t(17) = 2.67, p = .016$]. Thus, this latter

425 topographical scalp map explained most of the variance already two images before recognition,
 426 but then gradually decreased and was replaced by the concurrent occipital positivity/frontal
 427 positivity.

428 Next, we investigated whether these two dominant topographical maps were differentially
 429 influenced by memory, emotional content, or both factors concurrently. Regarding the occipital
 430 positivity/frontal negativity topography, a 2(emotion) x 2 (memory) x 4 (recognition level)
 431 repeated measures ANOVA showed a significant memory x recognition level interaction [$F(3,$
 432 $51) = 3.28, p = .028, \eta_p^2 = .162$], but no significant effect of emotion [$F(1, 17) = 1.01, p = .330,$
 433 $\eta_p^2 = .056$]. A similar 2 x 2 x 4 ANOVA on the GEV values of the occipital positivity/frontal
 434 positivity map disclosed a significant main effects of memory [$F(1, 17) = 20.30, p < .001, \eta_p^2 =$
 435 $.544$], and a memory x recognition level interaction [$F(3, 51) = 3.36, p = .026, \eta_p^2 = .165$] but no
 436 significant effect of emotion [$F(1, 17) = 0.29, p = .596, \eta_p^2 = .017$].

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

446 A comparable 2 x 4 ANOVA was used for the GEV values obtained for the concurrent
 447 occipital positivity/frontal positivity topography. This analysis showed a significant main effect

448 of memory [$F(1, 17) = 20.30, p < .001, \eta_p^2 = .544$], as well as a significant memory x recognition
449 level interaction [$F(3, 51) = 3.36, p = .026, \eta_p^2 = .165$]. Post-hoc paired t-test revealed higher
450 GEV values for new relative to old condition, both one image before [$t(17) = 3.41, p = .003$] and
451 at recognition level [$t(17) = 4.12, p = .001$] (Fig. 4D). Thus, a comparable, gradual increase in
452 GEV was observed for new and old scenes, with higher values for new relative to old condition
453 one image before, as well as at time of recognition.

454 3.6. Source localization results

455 Using sLORETA (Pascual-Marqui, 2002) we performed statistical non-parametric mapping
456 (SnPM) analyses on the average activity estimated during the 402-522ms post-stimulus onset
457 interval, during which the main topographic change took place across the four recognition levels
458 (from three images before up to recognition). We first compared ERP activity for three images
459 before recognition to actual recognition (see Schettino et al., 2011, for a similar approach),
460 separately for new and old scenes. This analysis revealed, for new scenes, a stronger activation
461 for recognition relative to three images before in the dACC ($\pm 10x, +15y, +35z$) [$t(17) = 2.75, p =$
462 $.014$], whereas symmetrically stronger activity three images before compared to recognition was
463 found in the insula ($\pm 40x, +15y, 0z$) [$t(17) = -3.29, p = .004$] (Fig. 5, upper panel). On the other
464 hand, the SnPM analysis for old scenes showed stronger activity during recognition relative to
465 three images before recognition in a non-overlapping network of brain regions, including the
466 PHG ($\pm 29x, -49y, -6z$) [$t(17) = 4.46, p < .001$] and the fusiform gyrus (FG; $\pm 41x, -45y, -19z$)
467 [$t(17) = 4.02, p = .001$] (Fig. 5, lower panel). Therefore, these four brain areas (dACC, insula,
468 PHG, and FG) were defined as regions of interest (ROIs) for further analyses⁷. For each ROI
469 (defined as a sphere of 5 mm radius centered around the coordinates reported above), we

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

470 extracted the mean amplitude (current density) value during the same time interval (402-522 ms
471 following stimulus onset) and assessed, at the statistical level, effects of recognition level and
472 emotion.

473 3.6.1. *dACC and insula (new scenes)*

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

481 Inverse solution results obtained for the insula in the new condition revealed a similar
482 response profile (Fig. 6B). However, the emotional content of the scenes visibly influenced
483 reconstructed activity in this ROI, unlike the dACC. A 2 (emotion) x 4 (recognition level)
484 ANOVA disclosed a significant emotion x recognition level interaction [$F(3, 51) = 3.75, p =$
485 $.016, \eta_p^2 = .181$]. Post-hoc analyses showed, for neutral pictures, only a significant difference
486 between three images before and time of recognition [$t(17) = -2.34, p = .032$]. Therefore, activity
487 in the insula for neutral pictures was relatively stable until recognition. By contrast, emotional
488 scenes elicited significantly higher activity one image relative to two images before recognition
489 [$t(17) = -3.17, p = .006$]. Activity remained stable between three images and two images before
490 recognition, as well as between one image before and time of recognition ($ps > .05$) (Fig. 6B).

491 3.6.2. *PHG and FG (old scenes)*

492 The response profile of the PHG and FG during recognition of old scenes was reliably
493 different compared to the two previous ROIs (i.e., dACC and insula) identified primarily for the
494 processing of new scenes. Unlike a categorical difference between early vs. late stages of
495 accumulation of perceptual evidence, a linear increase in current source density was observed
496 when moving from three images before to actual recognition in the PHG and FG. A 2 (emotion) x
497 4 (recognition level) ANOVA on the extracted amplitude values for the PHG revealed significant
498 main effects of emotion [$F(1, 17) = 6.33, p = .022, \eta_p^2 = .271$] and recognition level [$F(3, 51) =$
499 $17.06, p < .001, \eta_p^2 = .501$]. Post-hoc comparisons showed higher activity three images before
500 recognition for neutral compared to emotional scenes [$t(17) = 2.96, p = .009$] (Fig. 6C).

501 The same analyses performed on the extracted amplitude values for the FG yielded
502 comparable results. The 2 (emotion) x 4 (recognition level) ANOVA showed significant main
503 effects of emotion [$F(1, 17) = 8.71, p = .009, \eta_p^2 = .339$] and recognition level [$F(3, 51) = 11.75,$
504 $p < .001, \eta_p^2 = .409$], as well as a significant emotion x recognition level interaction [$F(3, 51) =$
505 $3.62, p = .019, \eta_p^2 = .176$]. As was the case for the PHG, the FG showed higher activity for
506 neutral vs. emotional scenes three images before recognition [$t(17) = 5.62, p < .001$] (Fig. 6D).

507 4. Discussion

508 Using advanced EEG methods, we characterized the electrophysiological correlates of
509 proactive processes active during the recognition of complex visual scenes and conveying either
510 a neutral or an emotional (pleasant or unpleasant) content. We designed a task suited to explore
511 the temporal dynamics of these accumulation of evidence processes, and eventually assessed
512 whether the emotional content of the scenes could reliably modulate their expression or not.
513 Each trial started with the presentation of a colorful neutral or emotional scene to be encoded in
514 short-term memory, followed by the gradual unfolding of the same scene content, a new one, or a

515 scrambled picture. Participants had to decide whether the progressively unfolded scene had the
516 same identity than the one shown at encoding or not. Moreover, we occasionally asked
517 participants to explicitly rate the emotional valence of the pictures, a manipulation that was
518 meant to promote the overt processing of the emotional content of the scenes throughout the
519 experiment. These ratings confirmed that participants correctly discriminated the emotional
520 content of the scenes. Likewise, results obtained for the LPP component at encoding further
521 corroborated this conclusion (see Fig. 2). Interestingly, a number of important new results
522 emerge from this study regarding possible modulatory effects of emotion on the online
523 generation of guesses or predictions during overt scene recognition, as discussed here below.

524 4.1. *Prolonged exploration for emotional compared to neutral scenes*

525 Behavioral results revealed that old scenes were recognized systematically earlier than new
526 scenes (Fig. 1B), providing direct evidence for the use of abstract visual representations during
527 unfolding, which were directly shaped by information provided to participants at encoding.
528 Moreover, we replicated our previous results (Schettino et al., 2011) and found that, regardless of
529 the memory status of the scenes (old vs. new), participants dwelt longer on emotional compared
530 to neutral scenes (Fig. 1B). As argued in Schettino et al. (2012), delayed recognition for
531 emotional relative to neutral scenes could be explained by differential motivational drives
532 between these two categories, including *positivity offset* (Cacioppo and Gardner, 1999; Cacioppo
533 et al., 1999, 1997; Norris et al., 2010). According to this general motivational account,
534 participants are usually inclined to engage in exploratory behavior when encountering emotion-
535 laden stimuli (especially pleasant ones), presumably because of their intrinsic rewarding value.
536 Interestingly, the use of mildly arousing scenes in our study, as opposed to mutilations or erotica,
537 may have boosted this asymmetry in motivational exploratory strategies between emotional and

538 neutral scenes. This motivational effect found in a sample of healthy women was similar for old
539 and new scenes, suggesting that effects of emotion on proactive guesses during scene recognition
540 probably occurred either before or after the input stimulus was compared against existing visual
541 representations stored in (short-term) memory. Alternatively, emotion could somehow interfere
542 with these accumulation of evidence processes (at different moments depending either on the
543 presence or absence of an existing short-term memory trace for these scenes), in the sense that
544 the emotional content of the scenes would exert an extra source of variability and/or uncertainty
545 on these processes, compared to neutral scenes. In this view, the compelling processing of the
546 emotional content of the scenes (at encoding), which is reinforced by the use of an emotion
547 categorization task (based on the valence), leads to the activation of mental processes that are
548 probably shared in part with brain processes responsible for the accumulation of evidence,
549 eventually slowing down the recognition of these emotional scenes. Our new source localization
550 results indirectly confirm this assumption (see below).

551 *4.2. New and old scenes recruit non-overlapping brain networks during proactive visual*
552 *processes*

553 The control analysis performed on the mean amplitude of the centro-parietal old/new ERP
554 component recorded at time of recognition in a 500-750ms time window post-stimulus onset
555 showed significantly larger positive values for old relative to new scenes. These results are
556 consistent with previous studies (Curran and Cleary, 2003; Curran and Doyle, 2011; Weymar et
557 al., 2009; Wilding and Rugg, 1996; Wilding et al., 1995), and provide converging evidence that
558 our short-term memory manipulation was successful. However, neither the main effect of
559 emotion nor the emotion x memory interaction were significant (all $ps > .05$), indicating
560 comparable old/new effects for neutral and emotional scenes. This result might be explained by

561 the use of a short retention interval in the present experimental paradigm, as opposed to previous
562 ERP studies using intermediate (e.g., 1 week; Weymar et al., 2010, 2009) or long (e.g., 1 year;
563 Bradley et al., 1992; Dolcos et al., 2005; Weymar et al., 2011) retention intervals. Moreover,
564 interacting effects of emotion and memory were revealed in our study, but when considering
565 global topographical changes and their estimated generators in the inverse solution space.

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

584 4.3. *Modulatory effect of emotion depends on memory*

585 In agreement with the assumption of non-overlapping brain networks between new and old
586 scenes, our complementary source localization analysis confirmed that the processing of old
587 scenes was mostly achieved by a distributed network of ventral brains regions, including the
588 PHG and FG, whereas the processing of new scenes involved mainly neural changes in more
589 dorsal brain regions at the same latency, including the dACC and the insula. Interestingly, we
590 found that activity extracted in these ROIs was influenced by the emotional content of the
591 scenes, though at different stages during the accumulation of evidence depending on the actual
592 memory status of these scenes. These results suggest that emotion may exert pervasive effects on
593 these proactive processes during scene recognition. Accordingly, the estimation of the neural
594 sources of the ERP signal using a linear distributed inverse space turned out to be more sensitive
595 to capture subtle changes related to the processing of the emotional content of the scenes,
596 compared to the topographical mapping analyses carried out using 128 channels (Esslen et al.,
597 2004; Pascual-Marqui et al., 2002). This dissociation is not surprising though, given the
598 enhanced spatial sensitivity of distributed source localization methods (including sLORETA) that
599 enables to reveal subtle differences between experimental conditions, which may be otherwise
600 difficult to capture based on local amplitude measurements performed at the sensor level
601 (Brodbeck et al., 2011; Lantz et al., 2001; Michel and Murray, 2012).

602 4.4. *Enhanced uncertainty during the processing of new scenes*

603 Activity in the dACC for neutral scenes was low and close to baseline until one image before
604 recognition, when a sharp increase took place (see Fig. 6A). This specific response profile for the
605 dACC, which is consistent with the involvement of this medial frontal region in higher-order
606 decision making processes (Bush et al., 2002; Ridderinkhof et al., 2004; Seo and Lee, 2007), was

607 already found in previous imaging studies looking at accumulation of evidence processes taking
608 place during object or scene recognition (Ploran et al., 2011, 2007; Wheeler et al., 2008). This
609 sharp increase in the dACC close to recognition could reflect either uncertainty or conflict, given
610 the urge to stop the stimulus sequence and take a decision before the sequence comes to an end,
611 while the accumulated sensory evidence may not be completed yet (Anderson et al., 2009;
612 Philiastides and Sajda, 2007; Sohn et al., 2007). Interestingly, a similar effect in the dACC was
613 already reported in our previous ERP study, though based on a different task (Schettino et al.,
614 2011). Hence, this region may be involved in the coding of conflict or uncertainty during
615 perceptual decision making tasks at a more general level (Ridderinkhof et al., 2004; Ullsperger et
616 al., 2004), particularly when recognition targets are embedded in an emotional context (Kanske
617 and Kotz, 2011a, 2011b).

618 Not only the dACC, but also the insula showed increased activity in response to new scenes,
619 although it additionally showed a modulation according to the emotional content of the scenes
620 (Fig. 6B). Activation of the insula has previously been reported for a variety of tasks and stimuli
621 (Craig, 2009), including when exogenous sensory stimuli acquire salience (Seeley et al., 2007),
622 as well as in response to challenging and uncertain perceptual tasks (Grinband et al., 2006;
623 Philiastides and Sajda, 2007). Likewise, previous ERP work based on a similar approach as used
624 here already source-localized the insula during the early processing of response errors during a
625 speeded go/no-go task (Dhar et al., 2011). Presumably, similar effects could explain the
626 involvement of the insula in our task during the accumulation of perceptual evidence prior to
627 recognition. Whereas uncertainty likely decreased as a function of accumulation of evidence, at
628 time of recognition this process is perhaps not completed yet. Noteworthy, emotional stimuli
629 could somehow exacerbate this process in the insula, thereby shifting the neural response earlier

630 in time -- probably because of their intrinsic motivational salience -- compared to neutral stimuli.
631 Presumably, the emotional content of the stimulus might actively interfere with task demands
632 (memory matching task), resulting in an earlier experience of uncertainty or conflict for
633 emotional compared to neutral scenes.

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

641 *4.5. Emotion-dependent monotonic accumulation of perceptual evidence in ventral object-*
642 *selective regions during the processing of old scenes*

643 While the processing of new scenes was selectively associated with specific neural effects in
644 the dACC and insula starting 400 ms post-stimulus onset, a different picture emerged for the
645 processing of old scenes at the same latency, where ventral object-sensitive brain regions were
646 found to be significantly more active. Among them, activity in the PHG increased linearly as a
647 function of accumulation of evidence, with the lowest amplitude values three images before
648 recognition and the highest at time of recognition (see Fig. 6C). Given the ubiquitous
649 involvement of this specific brain area in the processing of contextual information needed for
650 successful scene recognition (Bar and Aminoff, 2003; Bar et al., 2008; Kveraga et al., 2011), we
651 interpreted our new results as reflecting similar mechanisms. The linear trend found in this
652 region during accumulation of evidence prior to recognition (see also Schettino et al., 2011) is

653 consistent with the assumption that this region is rapidly involved in the analysis of diagnostic
654 contextual information, primarily conveyed by magnocellular input (Bar, 2009, 2007, 2004).
655 Interestingly, we found that this response profile was not identical for emotional compared to
656 neutral scenes. More specifically, during early stages of accumulation of evidence (i.e., three
657 images before recognition), the amplitude of the PHG was significantly lower for emotional
658 compared to neutral scenes. An early interference effect probably took place for emotional
659 scenes, eventually preventing the initiation of the generative accumulation of evidence process
660 (presumably based on contextual information carried by LSF cues) taking place in this region.
661 However, because at time of recognition this amplitude difference between neutral and emotional
662 scenes was no longer significant, it is likely that a more rapid accumulation of evidence took
663 place in this region for emotional compared to neutral scenes. Hence, emotional factors would
664 initially interfere with the processing of diagnostic contextual information (based on the
665 extraction of LSF cues), but later boost this same process when more evidence is timely gathered
666 and accumulated (Fig. 6C), presumably based on the concurrent processing of HSF information.
667 Such an interpretation is compatible with mounting evidence showing the importance of
668 contextual visual information during emotional scene recognition (Barrett and Kensinger, 2010;
669 Barrett et al., 2011; de Gelder et al., 2006; Righart and de Gelder, 2008, 2006; Righart and De
670 Gelder, 2008). Thus, due to their enhanced motivational relevance, emotional scenes led to a
671 steeper accumulation of evidence in the PHG relative to neutral scenes.

672 A comparable outcome was found for the FG (Fig. 6D). Previous imaging studies already
673 reported the involvement of the FG in the gradual accumulation of perceptual evidence (James et
674 al., 2000; Malach et al., 1995). Presumably, a similar accumulation of evidence mechanism took
675 place in the FG in our study, although one may argue that the diagnostic visual information used

676 by this region may be different compared to the PHG. More specifically, the FG could be
677 involved in the accumulation of perceptual evidence based on the rapid extraction of invariant
678 object features or viewpoint information, as opposed to contextual information in the PHG
679 (Epstein et al., 1999; Grill-Spector and Malach, 2004; Malach et al., 1995; Pourtois et al., 2010,
680 2005).

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

688 4.6. *Conclusion*

689 The results of this study shed light on the electrophysiological correlates (and the estimated
690 brain sources) of accumulation of perceptual evidence prior to scene recognition. Four hundred
691 ms following stimulus onset, regions in the dACC and insula were selectively active prior to
692 overt recognition of new scenes, likely translating either enhanced uncertainty or conflict
693 monitoring during perceptual decision making. Interestingly, activity in the insula was elicited
694 earlier for emotional compared to neutral scenes, suggesting prioritized processing for this class
695 of stimuli due to their enhanced motivational salience, particularly in perceptually ambiguous
696 tasks. By contrast, at the same latency following stimulus onset, old scenes recruited primarily
697 ventral object-selective regions during accumulation of perceptual evidence, including the PHG
698 and FG. Interestingly, an early modulation of their response profile as a function of the emotional

699 content of the scenes was observed. Accordingly, even though neural mechanisms underlying
700 accumulation of evidence during scene recognition are multiple and can be dissociated based on
701 memory (i.e., old vs. new scenes), it is striking to observe that emotion exerts pervasive
702 interference effects on these proactive processes during fairly early stages of accumulation of
703 perceptual evidence (when the retinal input is still minimal or impoverished). Our new ERP
704 findings are consistent with a recent theoretical proposal (Barrett and Bar, 2009) suggesting that
705 the affective properties of the visual input are intrinsically embedded in the predictions generated
706 during the rapid extraction of its gist. Given the direct anatomical projections from specific
707 medial frontal brain areas (including the ACC and insula) -- active during recognition processes--
708 to autonomic and endocrine output centers in the hypothalamus, midbrain, and brainstem,
709 internal affective states of the organism might potentially be one feature of the set of predictions
710 used to facilitate recognition (Bar and Aminoff, 2003; Bar, 2004; Barrett and Bar, 2009).

711

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References

- Anderson, Anderson, J.F., Ferris, J.L., Fincham, J.M., Jung, K.J., 2009. Lateral inferior prefrontal cortex and anterior cingulate cortex are engaged at different stages in the solution of insight problems. *P Natl Acad Sci USA* 106, 10799–10804.
- Bar, M., 2003. A cortical mechanism for triggering top-down facilitation in visual object recognition. *Journal of Cognitive Neuroscience* 15, 600–609.
- Bar, M., 2004. Visual objects in context. *Nature Reviews Neuroscience* 5, 617–629.
- Bar, M., 2007. The proactive brain: using analogies and associations to generate predictions. *Trends Cogn Sci* 11, 280–9.
- Bar, M., 2009. The proactive brain: memory for predictions. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364, 1235–1243.
- Bar, M., Aminoff, E., 2003. Cortical analysis of visual context. *Neuron* 38, 347–358.
- Bar, M., Aminoff, E., Schacter, D.L., 2008. Scenes unseen: The parahippocampal cortex intrinsically subserves contextual associations, not scenes or places per se. *Journal of Neuroscience* 28, 8539–8544.
- Barrett, L.F., Bar, M., 2009. See it with feeling: affective predictions during object perception. *Philos Trans R Soc Lond B Biol Sci* 364, 1325–34.
- Barrett, L.F., Kensinger, E.A., 2010. Context Is Routinely Encoded During Emotion Perception. *Psychological Science* 21, 595–599.
- Barrett, L.F., Mesquita, B., Gendron, M., 2011. Context in Emotion Perception. *Current Directions in Psychological Science* 20, 286–290.
- Barrett, L.F., Mesquita, B., Ochsner, K.N., Gross, J.J., 2007. The experience of emotion. *Annual Review of Psychology* 58, 373–403.

- Bradley, M.M., Greenwald, M.K., Petry, M.C., Lang, P.J., 1992. Remembering Pictures: Pleasure and Arousal in Memory. *Journal of Experimental Psychology-Learning Memory and Cognition* 18, 379–390.
- Bradley, M.M., Lang, P.J., 1994. Measuring Emotion: The Self-Assessment Mannequin and the Semantic Differential. *Journal of Behavior Therapy and Experimental Psychiatry* 25, 49–59.
- Brandeis, D., Lehmann, D., Michel, C.M., Mingrone, W., 1995. Mapping event-related brain potential microstates to sentence endings. *Brain Topography* 8, 145–59.
- Brodbeck, V., Spinelli, L., Lascano, A.M., Wissmeier, M., Vargas, M.I., Vulliemoz, S., Pollo, C., Schaller, K., Michel, C.M., Seeck, M., 2011. Electroencephalographic source imaging: a prospective study of 152 operated epileptic patients. *Brain* 134, 2887–2897.
- Brunet, D., Murray, M.M., Michel, C.M., 2011. Spatiotemporal Analysis of Multichannel EEG: CARTOOL. *Computational Intelligence and Neuroscience* 2011.
- Bullier, J., 2001. Integrated model of visual processing. *Brain Res Rev* 36, 96–107.
- Bush, G., Vogt, B.A., Holmes, J., Dale, A.M., Greve, D., Jenike, M.A., Rosen, B.R., 2002. Dorsal anterior cingulate cortex: A role in reward-based decision making. *P Natl Acad Sci USA* 99, 523–528.
- Cacioppo, J.T., Gardner, W.L., 1999. Emotion. *Annual Review of Psychology* 50, 191–214.
- Cacioppo, J.T., Gardner, W.L., Berntson, G.G., 1997. Beyond Bipolar Conceptualizations and Measures: The Case of Attitudes and Evaluative Space. *Personality and Social Psychology Review* 1, 3–25.

- Cacioppo, J.T., Gardner, W.L., Berntson, G.G., 1999. The affect system has parallel and integrative processing components: Form follows function. *J Pers Soc Psychol* 76, 839–855.
- Carlson, T., Grol, M.J., Verstraten, F.A.J., 2006. Dynamics of visual recognition revealed by fMRI. *Neuroimage* 32, 892–905.
- Courtney, S.M., Ungerleider, B.G., Keil, K., Haxby, J.V., 1997. Transient and sustained activity in a distributed neural system for human working memory. *Nature* 386, 608–611.
- Craig, A.D., 2009. How do you feel - now? The anterior insula and human awareness. *Nature Reviews Neuroscience* 10, 59–70.
- Curran, T., Cleary, A.M., 2003. Using ERPs to dissociate recollection from familiarity in picture recognition. *Cognitive Brain Research* 15, 191–205.
- Curran, T., Doyle, J., 2011. Picture Superiority Doubly Dissociates the ERP Correlates of Recollection and Familiarity. *Journal of Cognitive Neuroscience* 23, 1247–1262.
- Damaraju, E., Huang, Y.M., Barrett, L.F., Pessoa, L., 2009. Affective learning enhances activity and functional connectivity in early visual cortex. *Neuropsychologia* 47, 2480–2487.
- De Gelder, B., Meeren, H.K.M., Righart, R., Van den Stock, J., Van de Riet, W.A.C., Tamietto, M., 2006. Beyond the face: exploring rapid influences of context on face processing. *Visual Perception, Pt 2: Fundamentals of Awareness: Multi-Sensory Integration and High-Order Perception* 155, 37–48.
- Delplanque, S., N'diaye, K., Scherer, K., Grandjean, D., 2007. Spatial frequencies or emotional effects? A systematic measure of spatial frequencies for IAPS pictures by a discrete wavelet analysis. *Journal of Neuroscience Methods* 165, 144–150.

- Dhar, M., Wiersema, J.R., Pourtois, G., 2011. Cascade of Neural Events Leading from Error Commission to Subsequent Awareness Revealed Using EEG Source Imaging. *Plos One* 6.
- Dolcos, F., Cabeza, R., 2002. Event-related potentials of emotional memory: encoding pleasant, unpleasant, and neutral pictures. *Cogn Affect Behav Neurosci* 2, 252–63.
- Dolcos, F., LaBar, K.S., Cabeza, R., 2005. Remembering one year later: role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. *Proc. Natl. Acad. Sci. U.S.A.* 102, 2626–2631.
- Dosenbach, N.U.F., Fair, D.A., Cohen, A.L., Schlaggar, B.L., Petersen, S.E., 2008. A dual-networks architecture of top-down control. *Trends in Cognitive Sciences* 12, 99–105.
- Epstein, R., Harris, A., Stanley, D., Kanwisher, N., 1999. The parahippocampal place area: recognition, navigation, or encoding? *Neuron* 23, 115–25.
- Esslen, M., Pascual-Marqui, R.D., Hell, D., Kochi, K., Lehmann, D., 2004. Brain areas and time course of emotional processing. *Neuroimage* 21, 1189–1203.
- Everaert, T., Spruyt, A., De Houwer, J., 2011. On the (Un)conditionality of Automatic Attitude Activation: The Valence Proportion Effect. *Canadian Journal of Experimental Psychology-Revue Canadienne De Psychologie Experimentale* 65, 125–132.
- Foti, D., Hajcak, G., Dien, J., 2009. Differentiating neural responses to emotional pictures: Evidence from temporal-spatial PCA. *Psychophysiology* 46, 521–530.
- Fuchs, M., Kastner, J., Wagner, M., Hawes, S., Ebersole, J.S., 2002. A standardized boundary element method volume conductor model. *Clin Neurophysiol* 113, 702–712.
- Goldman-Rakic, P.S., 1990. Cellular and circuit basis of working memory in prefrontal cortex of nonhuman primates. *Prog Brain Res* 85, 325–35; discussion 335–6.

- Gratton, G., Coles, M.G.H., Donchin, E., 1983. A New Method for Off-Line Removal of Ocular Artifact. *Electroen Clin Neuro* 55, 468–484.
- Grill-Spector, K., Malach, R., 2004. The human visual cortex. *Annu Rev Neurosci* 27, 649–77.
- Grinband, J., Hirsch, J., Ferrera, V.P., 2006. A neural representation of categorization uncertainty in the human brain. *Neuron* 49, 757–763.
- Halgren, E., Raji, T., Marinkovic, K., Jousmaki, V., Hari, R., 2000. Cognitive response profile of the human fusiform face area as determined by MEG. *Cerebral Cortex* 10, 69–81.
- Hegd , J., 2008. Time course of visual perception: Coarse-to-fine processing and beyond. *Prog Neurobiol* 84, 405–439.
- Henson, R.N.A., Hornberger, M., Rugg, M.D., 2005. Further dissociating the processes involved in recognition memory: An fMRI study. *Journal of Cognitive Neuroscience* 17, 1058–1073.
- Ito, S., Stuphorn, V., Brown, J.W., Schall, J.D., 2003. Performance monitoring by the anterior cingulate cortex during saccade countermanding. *Science* 302, 120–122.
- James, T.W., Humphrey, G.K., Gati, J.S., Menon, R.S., Goodale, M.A., 2000. The effects of visual object priming on brain activation before and after recognition. *Curr Biol* 10, 1017–1024.
- Jurcak, V., Tsuzuki, D., Dan, I., 2007. 10/20, 10/10, and 10/5 systems revisited: Their validity as relative head-surface-based positioning systems. *Neuroimage* 34, 1600–1611.
- Kaestner, E.J., Polich, J., 2011. Affective recognition memory processing and event-related brain potentials. *Cognitive Affective & Behavioral Neuroscience* 11, 186–198.

- Kanske, P., Kotz, S.A., 2011a. Emotion Triggers Executive Attention: Anterior Cingulate Cortex and Amygdala Responses to Emotional Words in a Conflict Task. *Human Brain Mapping* 32, 198–208.
- Kanske, P., Kotz, S.A., 2011b. Emotion Speeds up Conflict Resolution: A New Role for the Ventral Anterior Cingulate Cortex? *Cerebral Cortex* 21, 911–919.
- Kveraga, K., Ghuman, A.S., Kassam, K.S., Aminoff, E.A., Hamalainen, M.S., Chaumon, M., Bar, M., 2011. Early onset of neural synchronization in the contextual associations network. *Proceedings of the National Academy of Sciences of the United States of America* 108, 3389–3394.
- Lang, P.J., 1995. The Emotion Probe: Studies of Motivation and Attention. *American Psychologist* 50, 372–385.
- Lang, P.J., Bradley, M.M., Cuthbert, B.N., 2008. International affective picture system (IAPS): Affective ratings of pictures and instruction manual. Technical Report A-8. University of Florida, Gainesville, FL.
- Lantz, G., Menendez, R.G.D., Andino, S.G., Michel, C.M., 2001. Noninvasive localization of electromagnetic epileptic activity. II. Demonstration of sublobar accuracy in patients with simultaneous surface and depth recordings. *Brain Topography* 14, 139–147.
- Lehmann, D., Skrandies, W., 1980. Reference-Free Identification of Components of Checkerboard-Evoked Multichannel Potential Fields. *Electroen Clin Neuro* 48, 609–621.
- Malach, R., Reppas, J.B., Benson, R.R., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R., Tootell, R.B.H., 1995. Object-Related Activity Revealed by Functional Magnetic-Resonance-Imaging in Human Occipital Cortex. *Proceedings of the National Academy of Sciences of the United States of America* 92, 8135–8139.

- Mayr, U., 2004. Conflict, consciousness, and control. *Trends in Cognitive Sciences* 8, 145–148.
- Mazziotta, J., Toga, A., Evans, A., Fox, P., Lancaster, J., Zilles, K., Woods, R., Paus, T., Simpson, G., Pike, B., Holmes, C., Collins, L., Thompson, P., MacDonald, D., Iacoboni, M., Schormann, T., Amunts, K., Palomero-Gallagher, N., Geyer, S., Parsons, L., Narr, K., Kabani, N., Le Goualher, G., Boomsma, D., Cannon, T., Kawashima, R., Mazoyer, B., 2001. A probabilistic atlas and reference system for the human brain: International Consortium for Brain Mapping (ICBM). *Philos T R Soc B* 356, 1293–1322.
- Michel, C.M., Murray, M.M., 2012. Towards the utilization of EEG as a brain imaging tool. *Neuroimage* 61, 371–385.
- Michel, C.M., Seeck, M., Landis, T., 1999. Spatiotemporal dynamics of human cognition. *News Physiol Sci* 14, 206–214.
- Michel, C.M., Thut, G., Morand, S., Khateb, A., Pegna, A.J., De Peralta, R.G., Gonzales, S., Seeck, M., Landis, T., 2001. Electric source imaging of human brain functions. *Brain Res Rev* 36, 108–118.
- Murray, M.M., Brunet, D., Michel, C.M., 2008. Topographic ERP analyses: A step-by-step tutorial review. *Brain Topogr* 20, 249–264.
- Nelson, S.M., Dosenbach, N.U.F., Cohen, A.L., Wheeler, M.E., Schlaggar, B.L., Petersen, S.E., 2010. Role of the anterior insula in task-level control and focal attention. *Brain Structure & Function* 214, 669–680.
- Norris, C.J., Gollan, J., Berntson, G.G., Cacioppo, J.T., 2010. The current status of research on the structure of evaluative space. *Biol Psychol* 84, 422–436.
- Öhman, A., Flykt, A., Esteves, F., 2001. Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology-General* 130, 466–478.

- Oliva, A., Torralba, A., 2007. The role of context in object recognition. *Trends in Cognitive Sciences* 11, 520–527.
- Paller, K.A., Hutson, C.A., Miller, B.B., Boehm, S.G., 2003. Neural manifestations of memory with and without awareness. *Neuron* 38, 507–516.
- Pascual-Marqui, R.D., 2002. Standardized low-resolution brain electromagnetic tomography (sLORETA): Technical details. *Method Find Exp Clin* 24, 5–12.
- Pascual-Marqui, R.D., Esslen, M., Kochi, K., Lehmann, D., 2002. Functional imaging with low-resolution brain electromagnetic tomography (LORETA): A review. *Methods and Findings in Experimental and Clinical Pharmacology* 24, 91–95.
- Pascual-Marqui, R.D., Michel, C.M., Lehmann, D., 1995. Segmentation of Brain Electrical Activity into Microstates: Model Estimation and Validation. *Ieee T Bio-Med Eng* 42, 658–665.
- Perrin, F., Pernier, J., Bertrand, O., Echallier, J.F., 1989. Spherical Splines for Scalp Potential and Current-Density Mapping. *Electroen Clin Neuro* 72, 184–187.
- Pessoa, L., 2008. On the relationship between emotion and cognition. *Nature Reviews Neuroscience* 9, 148–158.
- Pessoa, L., Kastner, S., Ungerleider, L.G., 2002. Attentional control of the processing of neutral and emotional stimuli. *Cognitive Brain Research* 15, 31–45.
- Philiastides, M.G., Sajda, P., 2007. EEG-informed fMRI reveals spatiotemporal characteristics of perceptual decision making. *Journal of Neuroscience* 27, 13082–13091.
- Ploran, E.J., Nelson, S.M., Velanova, K., Donaldson, D.I., Petersen, S.E., Wheeler, M.E., 2007. Evidence accumulation and the moment of recognition: Dissociating perceptual recognition processes using fMRI. *Journal of Neuroscience* 27, 11912–11924.

- Ploran, E.J., Tremel, J.J., Nelson, S.M., Wheeler, M.E., 2011. High Quality but Limited Quantity Perceptual Evidence Produces Neural Accumulation in Frontal and Parietal Cortex. *Cerebral Cortex* 21, 2650–2662.
- Pourtois, G., Delplanque, S., Michel, C., Vuilleumier, P., 2008. Beyond conventional event-related brain potential (ERP): Exploring the time-course of visual emotion processing using topographic and principal component analyses. *Brain Topogr* 20, 265–277.
- Pourtois, G., Grandjean, D., Sander, D., Vuilleumier, P., 2004. Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex* 14, 619–633.
- Pourtois, G., Schettino, A., Vuilleumier, P., 2012. Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. *Biological Psychology*.
- Pourtois, G., Schwartz, S., Seghier, M.L., Lazeyras, F., Vuilleumier, P., 2005. Portraits or people? Distinct representations of face identity in the human visual cortex. *J Cognitive Neurosci* 17, 1043–1057.
- Pourtois, G., Spinelli, L., Seeck, M., Vuilleumier, P., 2010. Modulation of Face Processing by Emotional Expression and Gaze Direction during Intracranial Recordings in Right Fusiform Cortex. *Journal of Cognitive Neuroscience* 22, 2086–2107.
- Ranganath, C., Rainer, G., 2003. Neural mechanisms for detecting and remembering novel events. *Nat Rev Neurosci* 4, 193–202.
- Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S., 2004. The role of the medial frontal cortex in cognitive control. *Science* 306, 443–447.
- Righart, R., De Gelder, B., 2006. Context influences early perceptual analysis of faces - An electrophysiological study. *Cerebral Cortex* 16, 1249–1257.

- Righart, R., De Gelder, B., 2008. Rapid influence of emotional scenes on encoding of facial expressions: an ERP study. *Social Cognitive and Affective Neuroscience* 3, 270–278.
- Righart, R., De Gelder, B., 2008. Recognition of facial expressions is influenced by emotional scene gist. *Cognitive Affective & Behavioral Neuroscience* 8, 264–272.
- Rugg, M.D., Curran, T., 2007. Event-related potentials and recognition memory. *Trends in Cognitive Sciences* 11, 251–257.
- Rugg, M.D., Mark, R.E., Walla, P., Schloerscheidt, A.M., Birch, C.S., Allan, K., 1998. Dissociation of the neural correlates of implicit and explicit memory. *Nature* 392, 595–598.
- Russell, J.A., 1980. A Circumplex Model of Affect. *Journal of Personality and Social Psychology* 39, 1161–1178.
- Sanquist, T.F., Rohrbaugh, J.W., Syndulko, K., Lindsley, D.B., 1980. Electrocortical signs of levels of processing: perceptual analysis and recognition memory. *Psychophysiology* 17, 568–76.
- Schettino, A., Loeys, T., Bossi, M., Pourtois, G., 2012. Valence-Specific Modulation in the Accumulation of Perceptual Evidence Prior to Visual Scene Recognition. *PloS One* 7, e38064.
- Schettino, A., Loeys, T., Delplanque, S., Pourtois, G., 2011. Brain dynamics of upstream perceptual processes leading to visual object recognition: A high density ERP topographic mapping study. *Neuroimage* 55, 1227–1241.
- Schupp, H., Flaisch, T., Stockburger, J., Junghöfer, M., 2006. Emotion and attention: Event-related brain potential studies. *Journal of Psychophysiology* 20, 115–115.

- Schupp, H.T., Cuthbert, B.N., Bradley, M.M., Hillman, C.H., Hamm, A.O., Lang, P.J., 2004a. Brain processes in emotional perception: Motivated attention. *Cognition & Emotion* 18, 593–611.
- Schupp, H.T., Junghöfer, M., Weike, A.I., Hamm, A.O., 2004b. The selective processing of briefly presented affective pictures: An ERP analysis. *Psychophysiology* 41, 441–449.
- Schupp, H.T., Stockburger, J., Bublitzky, F., Junghöfer, M., Weike, A.I., Hamm, A.O., 2003. The selective processing of affective pictures: Effects of emotion and attention. *Journal of Psychophysiology* 17, 178–178.
- Schupp, H.T., Stockburger, J., Codispoti, M., Junghöfer, M., Weike, A.I., Hamm, A.O., 2007. Selective visual attention to emotion. *Journal of Neuroscience* 27, 1082–1089.
- Seeley, W.W., Menon, V., Schatzberg, A.F., Keller, J., Glover, G.H., Kenna, H., Reiss, A.L., Greicius, M.D., 2007. Dissociable intrinsic connectivity networks for salience processing and executive control. *Journal of Neuroscience* 27, 2349–2356.
- Sekihara, K., Sahani, M., Nagarajan, S.S., 2005. Localization bias and spatial resolution of adaptive and non-adaptive spatial filters for MEG source reconstruction. *Neuroimage* 25, 1056–1067.
- Seo, H., Lee, D., 2007. Temporal filtering of reward signals in the dorsal anterior cingulate cortex during a mixed-strategy game. *J Neurosci* 27, 8366–8377.
- Silva, L.R., Amitai, Y., Connors, B.W., 1991. Intrinsic oscillations of neocortex generated by layer 5 pyramidal neurons. *Science* 251, 432–5.
- Sohn, M.H., Albert, M.V., Jung, K.J., Carter, C.S., Anderson, J.R., 2007. Anticipation of conflict monitoring in the anterior cingulate cortex and the prefrontal cortex. *P Natl Acad Sci USA* 104, 10330–10334.

- Spruyt, A., De Houwer, J., Hermans, D., Eelen, P., 2007. Affective priming of nonaffective semantic categorization responses. *Experimental Psychology* 54, 44–53.
- Sterzer, P., Kleinschmidt, A., 2010. Anterior insula activations in perceptual paradigms: often observed but barely understood. *Brain Structure & Function* 214, 611–622.
- Summerfield, C., Eger, T., 2009. Expectation (and attention) in visual cognition. *Trends in Cognitive Sciences* 13, 403–409.
- Tibshirani, R., Walther, G., 2005. Cluster validation by prediction strength. *Journal of Computational and Graphical Statistics* 14, 511–528.
- Todd, R.M., Cunningham, W.A., Anderson, A.K., Thompson, E., 2012. Affect-biased attention as emotion regulation. *Trends Cogn Sci* 16, 365–72.
- Treisman, A.M., Kanwisher, N.G., 1998. Perceiving visually presented objects: recognition, awareness, and modularity. *Curr Opin Neurobiol* 8, 218–226.
- Ullsperger, M., Volz, K.G., Von Cramon, D.Y., 2004. A common neural system signaling the need for behavioral changes. *Trends Cogn Sci* 8, 445–446.
- Voss, J.L., Paller, K.A., 2006. Fluent conceptual processing and explicit memory for faces are electrophysiologically distinct. *Journal of Neuroscience* 26, 926–933.
- Voss, J.L., Paller, K.A., 2008. Brain substrates of implicit and explicit memory: the importance of concurrently acquired neural signals of both memory types. *Neuropsychologia* 46, 3021–9.
- Vuilleumier, P., 2005. How brains beware: neural mechanisms of emotional attention. *Trends Cogn Sci* 9, 585–94.
- Weymar, M., Löw, A., Hamm, A.O., 2011. Emotional memories are resilient to time: evidence from the parietal ERP old/new effect. *Hum Brain Mapp* 32, 632–640.

- Weymar, M., Low, A., Melzig, C.A., Hamm, A.O., 2009. Enhanced long-term recollection for emotional pictures: evidence from high-density ERPs. *Psychophysiology* 46, 1200–7.
- Weymar, M., Löw, A., Modess, C., Engel, G., Gründling, M., Petersmann, A., Siegmund, W., Hamm, A.O., 2010. Propranolol selectively blocks the enhanced parietal old/new effect during long-term recollection of unpleasant pictures: a high density ERP study. *Neuroimage* 49, 2800–2806.
- Wheeler, M.E., Petersen, S.E., Nelson, S.M., Ploran, E.J., Velanova, K., 2008. Dissociating Early and Late Error Signals in Perceptual Recognition. *Journal of Cognitive Neuroscience* 20, 2211–2225.
- Wilding, E.L., Doyle, M.C., Rugg, M.D., 1995. Recognition Memory with and without Retrieval of Context - an Event-Related Potential Study. *Neuropsychologia* 33, 743–767.
- Wilding, E.L., Rugg, M.D., 1996. An event-related potential study of recognition memory with and without retrieval of source. *Brain* 119, 889–905.

715

Figure captions

716 Figure 1. (A) Procedure and task. Colorful neutral, unpleasant, and pleasant IAPS scenes (not
717 shown here for copyright reasons) were randomly presented to participants at the beginning of
718 each trial. After a mask, a grayscale version of the same scene, a new one, or a scrambled picture
719 was progressively revealed using six sequential steps. Each step added new low and high spatial
720 frequency information to the previous one, in a parametric fashion. Participants were required to
721 stop the sequence -- by pressing a button on the response box (Response1) -- as soon as they
722 could decide whether the content of the gradually unfolded scene was the one seen at the
723 beginning of the trial (i.e., colorful picture), a new one, or a scrambled picture. Participants
724 subsequently validated their choice and confirmed whether the scene was “old”, “new”, or
725 “scrambled” (Response2). (B) Behavioral results. Cumulative percentage of correct Responses1
726 as a function of the six image levels, separately for new (gray lines), old (black lines), neutral
727 (solid lines), and emotional (dashed lines) scenes. Vertical bars correspond to standard errors of
728 the mean. Results show that participants were able to perform the memory task significantly
729 earlier for old relative to new scenes, suggesting that less perceptual evidence was needed for the
730 former compared to the latter. Neutral scenes were recognized reliably earlier compared to
731 emotional scenes. No significant interaction effect between memory and emotion was found (see
732 main text).

733

734 Figure 2. Grand-average LPP recorded from a posterior parietal cluster of electrodes (average
735 of activity recorded from electrodes A8, A20, B5), separately for neutral (black line) and
736 emotional (red line; pleasant and unpleasant merged) scenes. The black vertical dashed line
737 indicates the onset of the colorful picture. The gray area indicates the time window during which

738 the mean amplitude of the LPP was measured (500-1000 ms post-stimulus onset). LPP was
739 significantly larger for emotional compared to neutral scenes.

740

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

748

749 Figure 4. Topographic mapping results. (A) Grand-average (N = 18) ERP waveforms,
750 obtained for the level corresponding to actual recognition (new scenes in black, old scenes in
751 red), for all 128 electrodes concurrently (butterfly). The green dashed vertical line indicates the
752 onset of the visual stimulus. The gray area indicates the time window (400-522 ms) during which
753 a reliable topographical change occurred. (B) Results of the spatiotemporal cluster analysis (0-
754 600 ms after stimulus onset) for the four main conditions (recognition, one image before, two
755 images before, and three images before recognition). A main solution with eight dominant
756 topographic maps was found to explain > 90% of the variance (for illustrative purposes, only the
757 most salient maps are highlighted). Scalp topographies of the N1 (in black) and P2 (in gray) ERP
758 components were shared across the four conditions, suggesting a similar low-level processing of
759 the visual stimulus. By contrast, in a time window spanning 402-522 ms following stimulus
760 onset, reliable topographic changes were observed between the four recognition levels. An

761 occipital positivity with a broad frontal negativity (in green) explained most of the variance up to
762 one image before recognition. Conversely, an occipital positivity with a focal frontal positivity
763 (in red) was already evidenced one image before recognition, being then predominant at time of
764 recognition. (C) Statistical results, obtained after the fitting procedure, for the GEV of the
765 occipital positivity/frontal negativity scalp map identified in the 402-522 ms time window
766 following stimulus onset (separately for new vs. old scenes). Results showed a sharp increase in
767 GEV from three images to two images before recognition, followed by a progressive decrease
768 until recognition. Furthermore, a higher GEV for new relative to old scenes was evidenced two
769 images before recognition. (D) On the other hand, a linear increase in GEV as a function of
770 recognition level was evident for the concurrent occipital positivity/frontal positivity topography.
771 A higher GEV was observed for new compared to old scenes one image before recognition, as
772 well as at recognition. * $p < .05$; ** $p < .01$; *** $p < .001$. Vertical bars correspond to standard
773 errors of the mean.

774

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

783

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

Figure 1A
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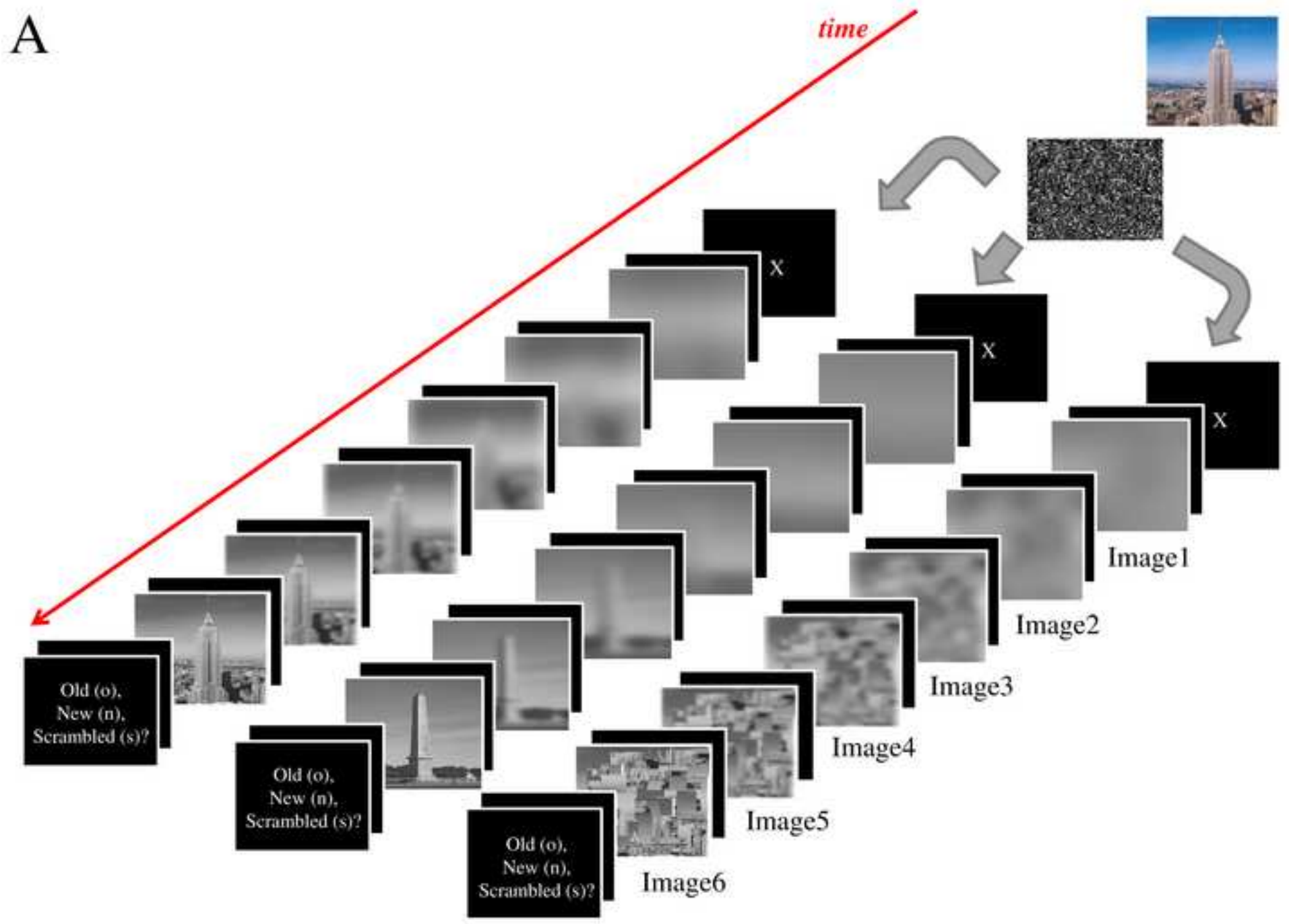


Figure 1B
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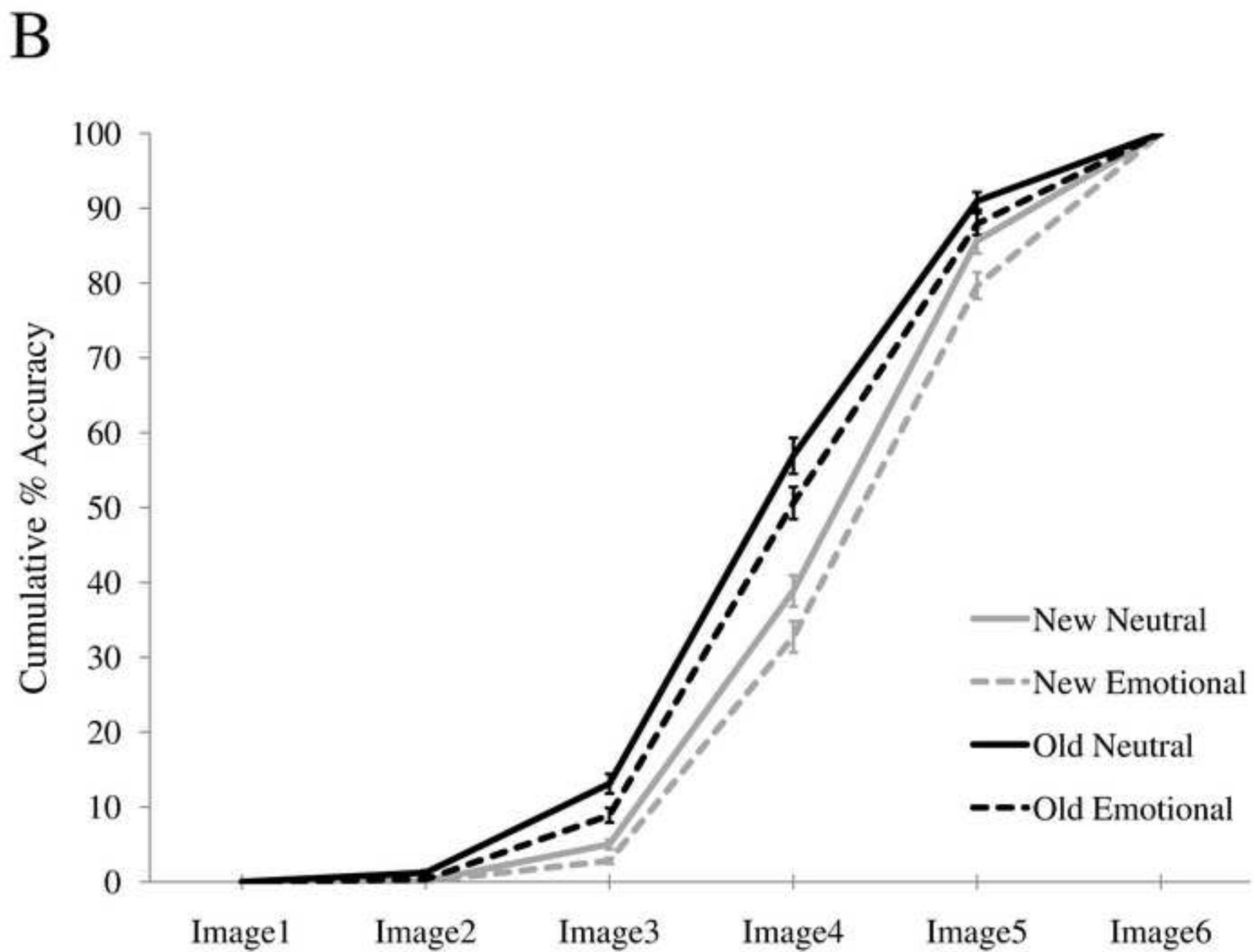


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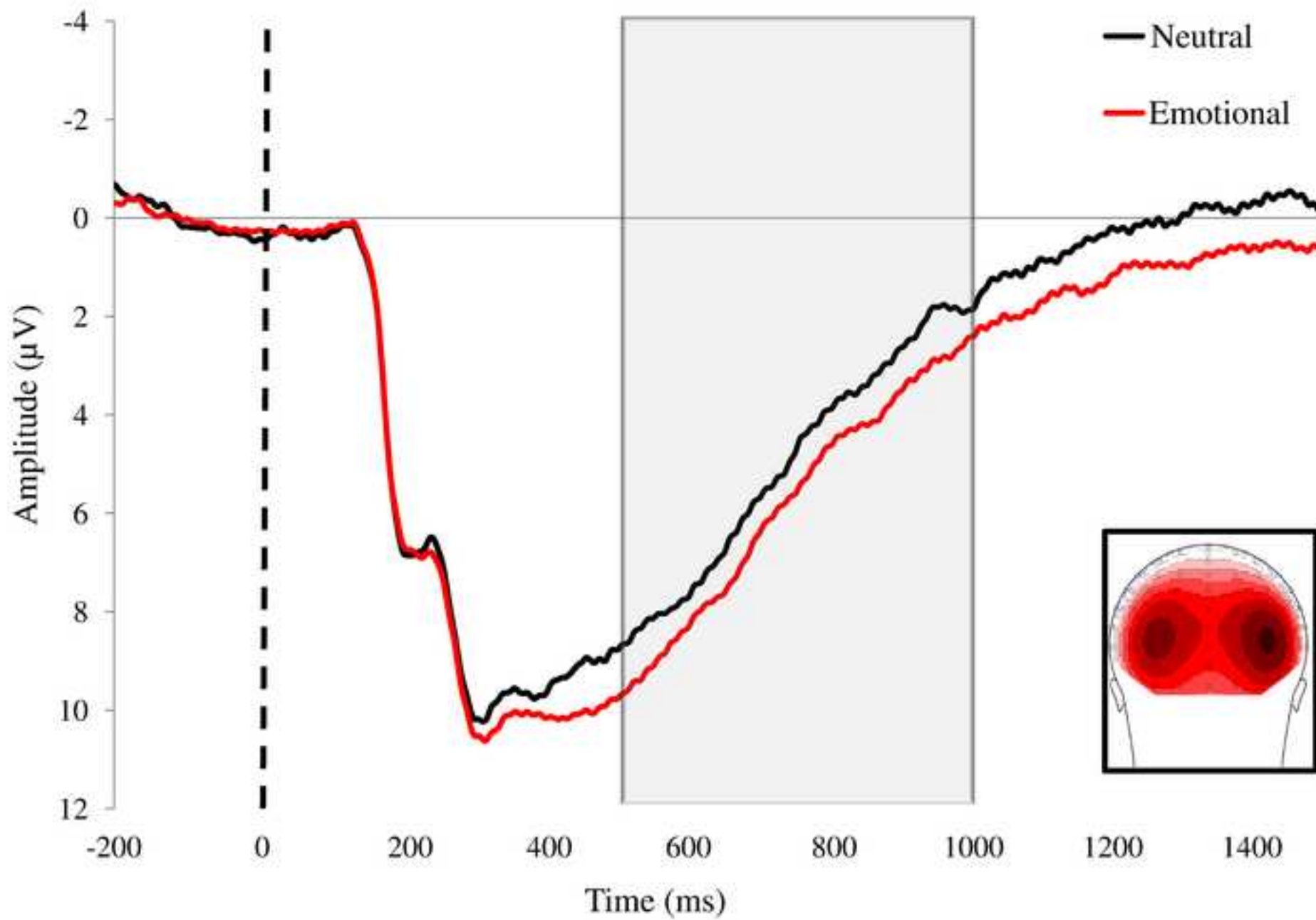


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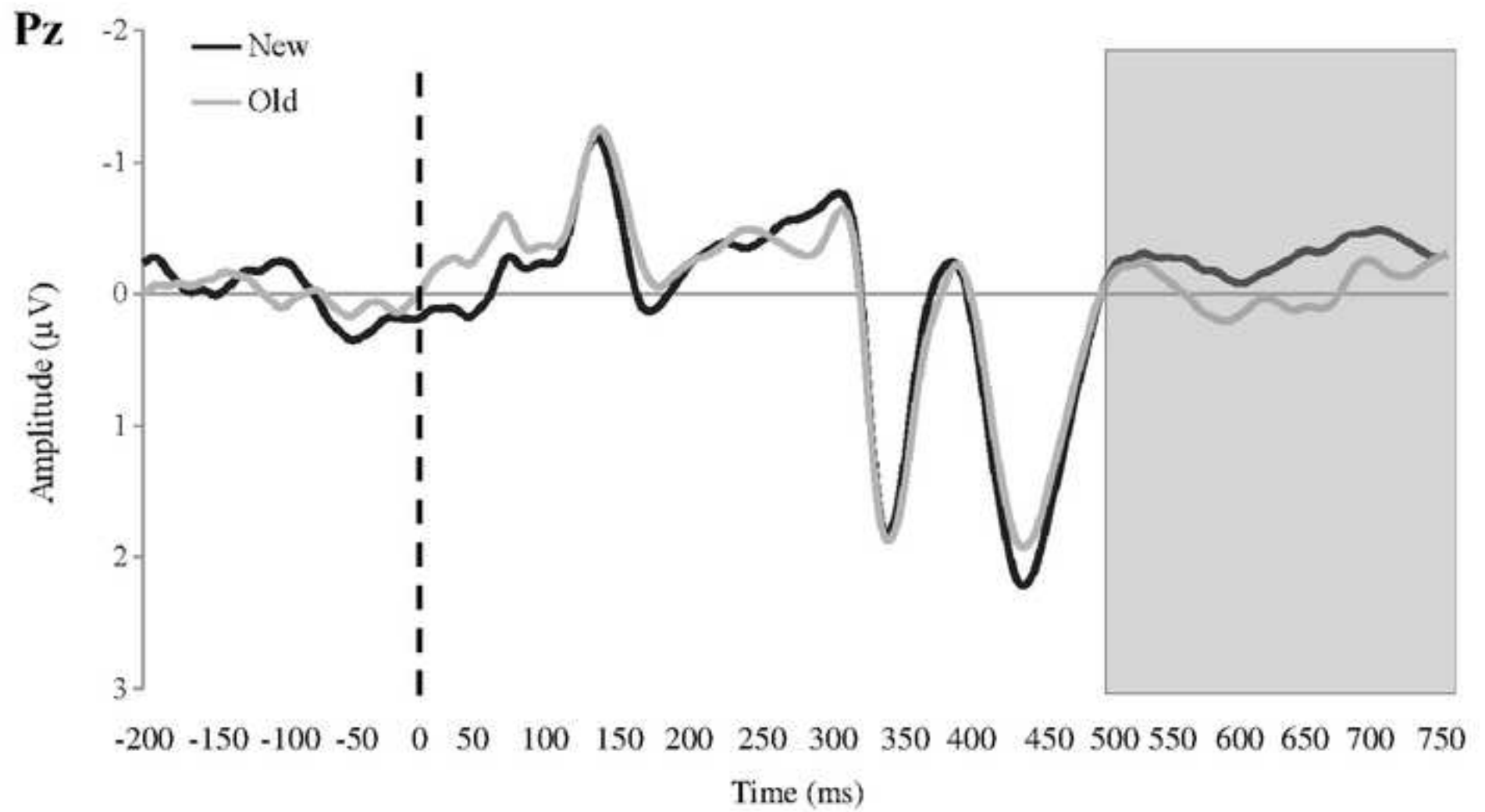


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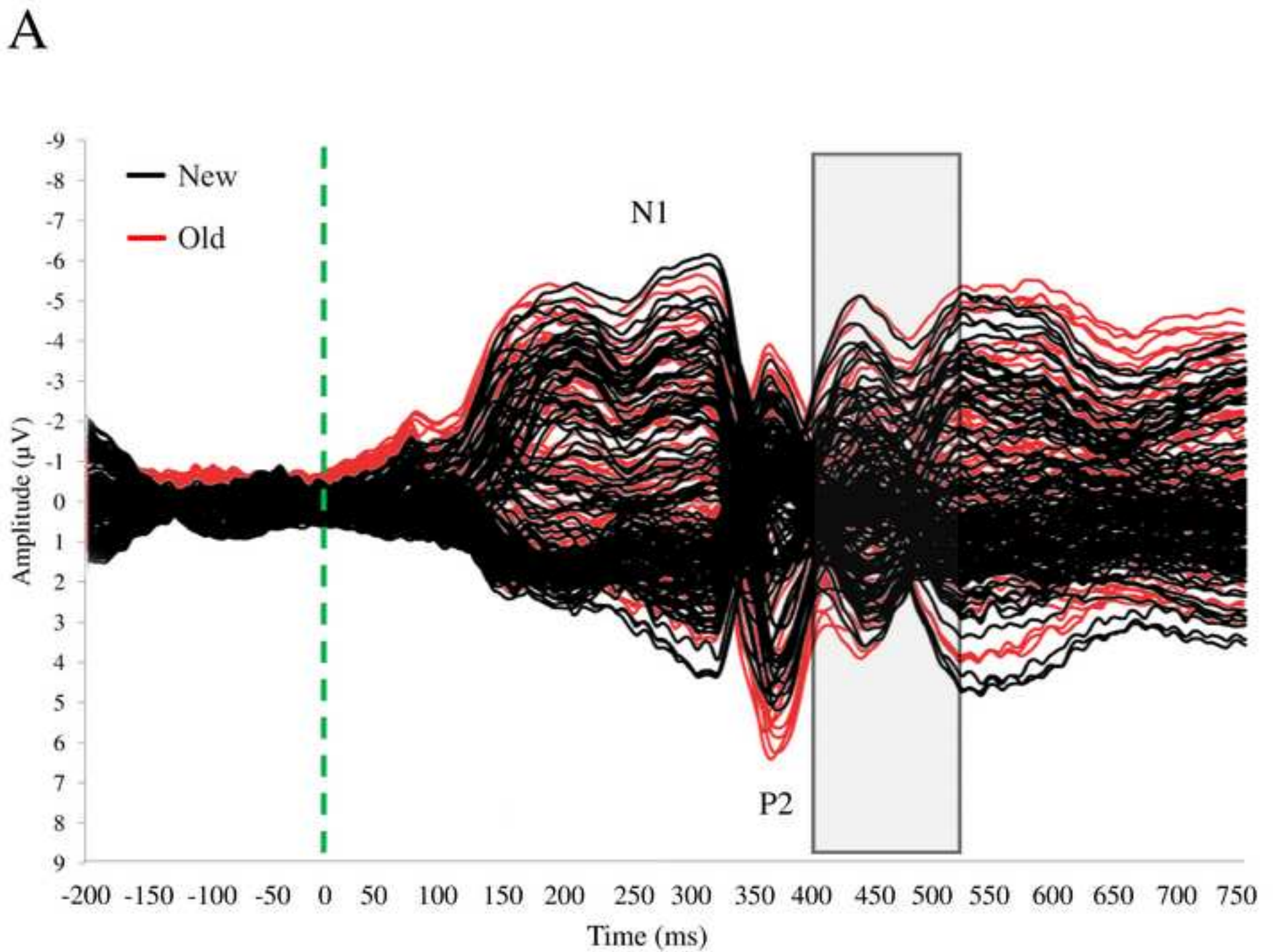


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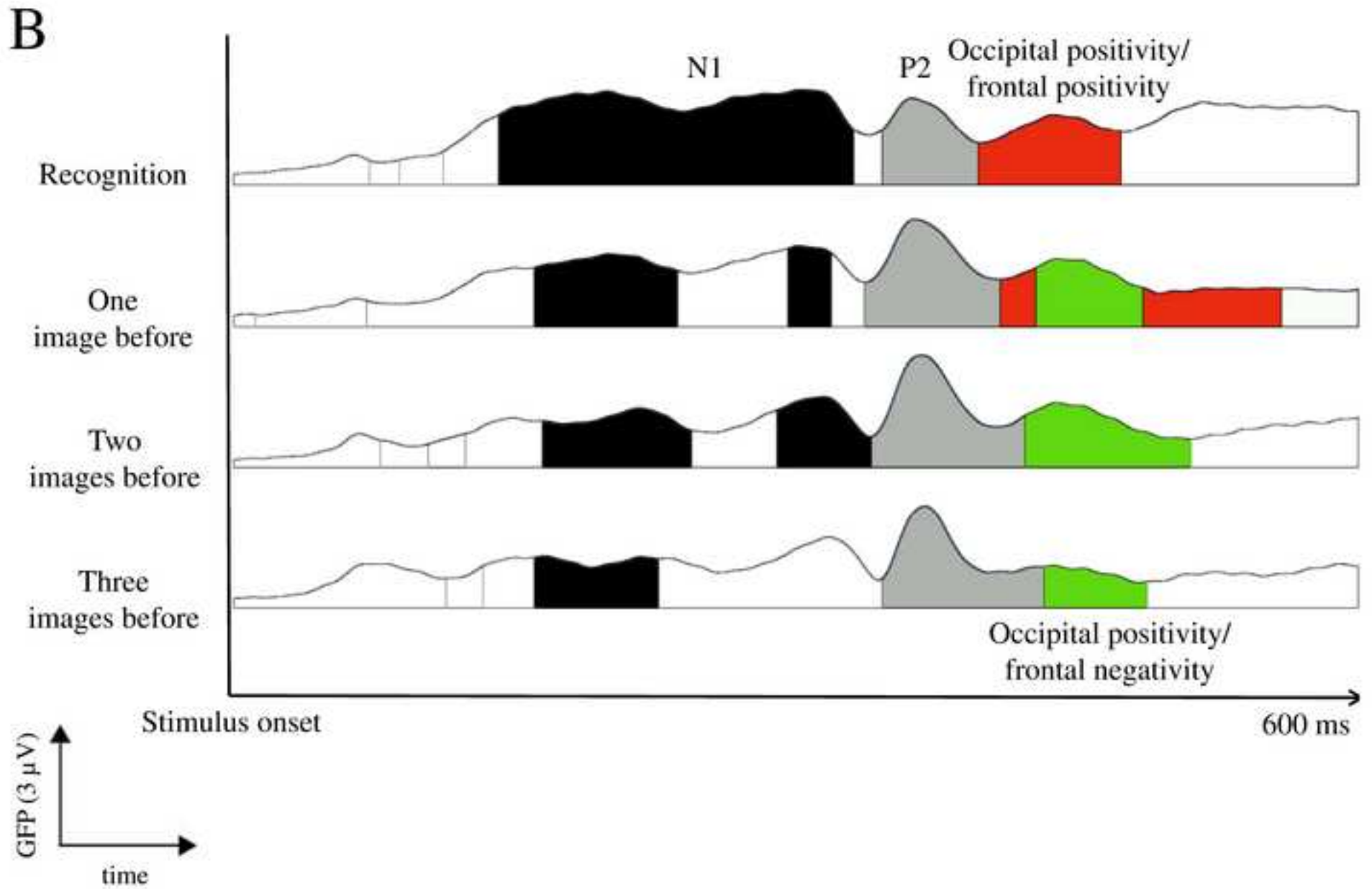


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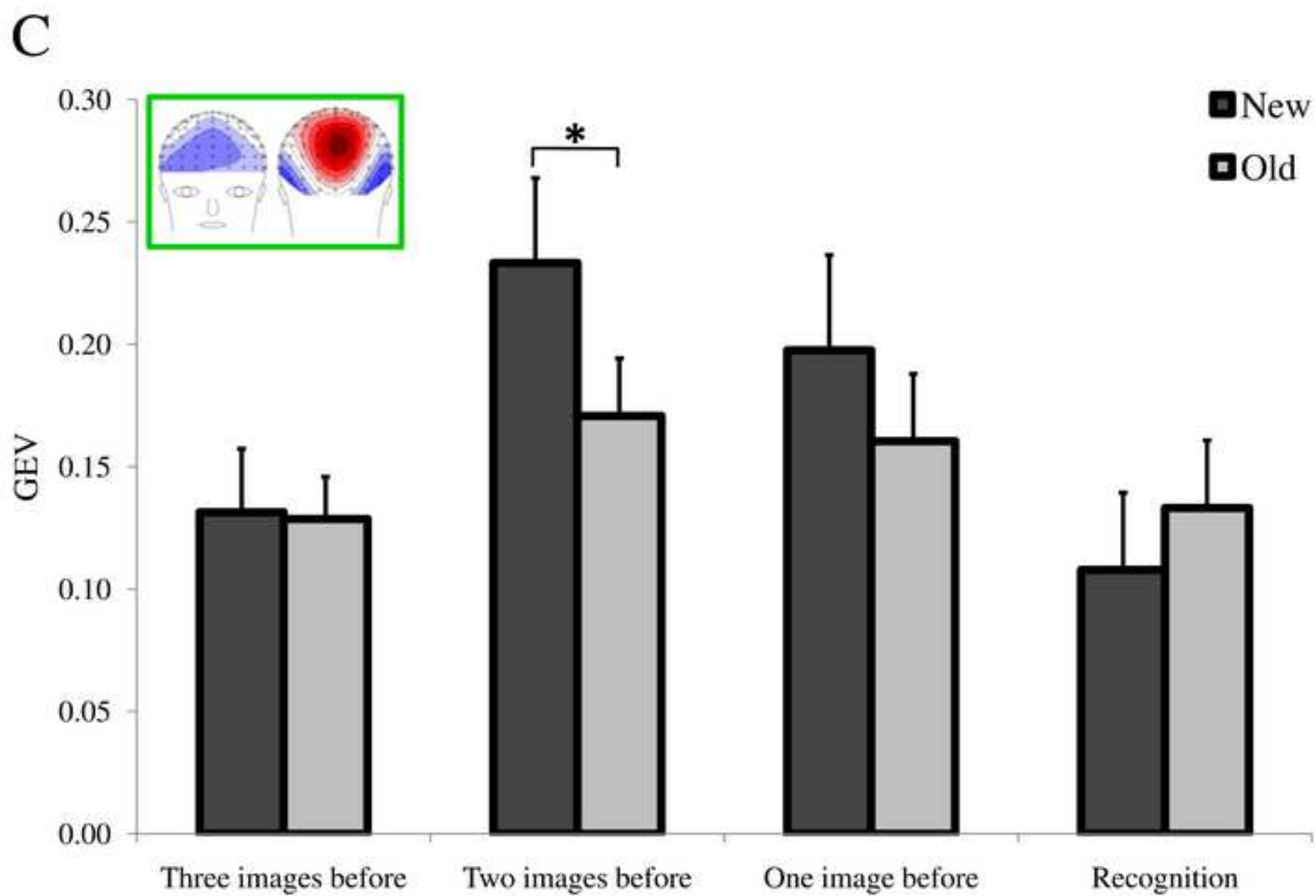


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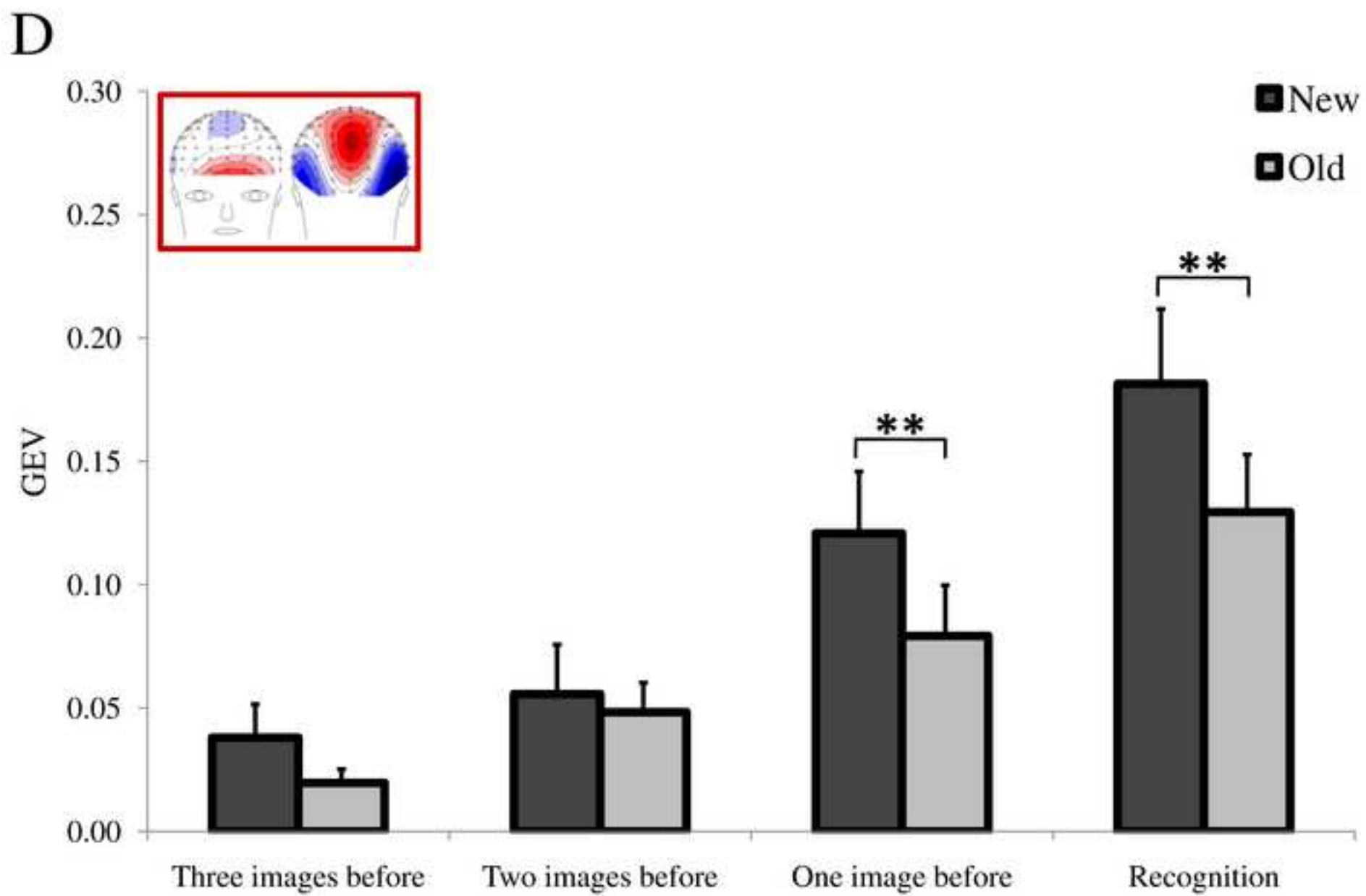


Figure 5
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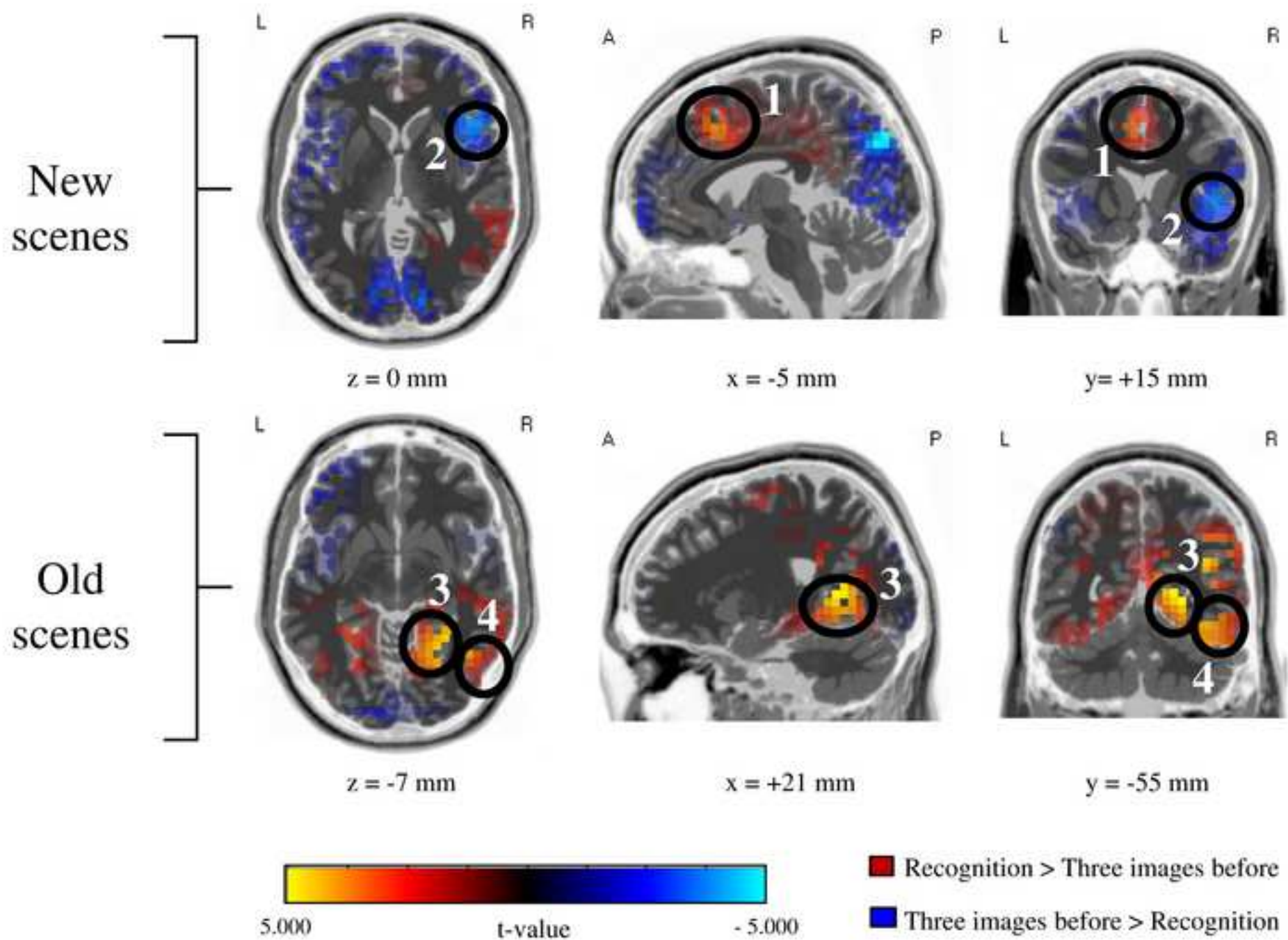


Figure 6A
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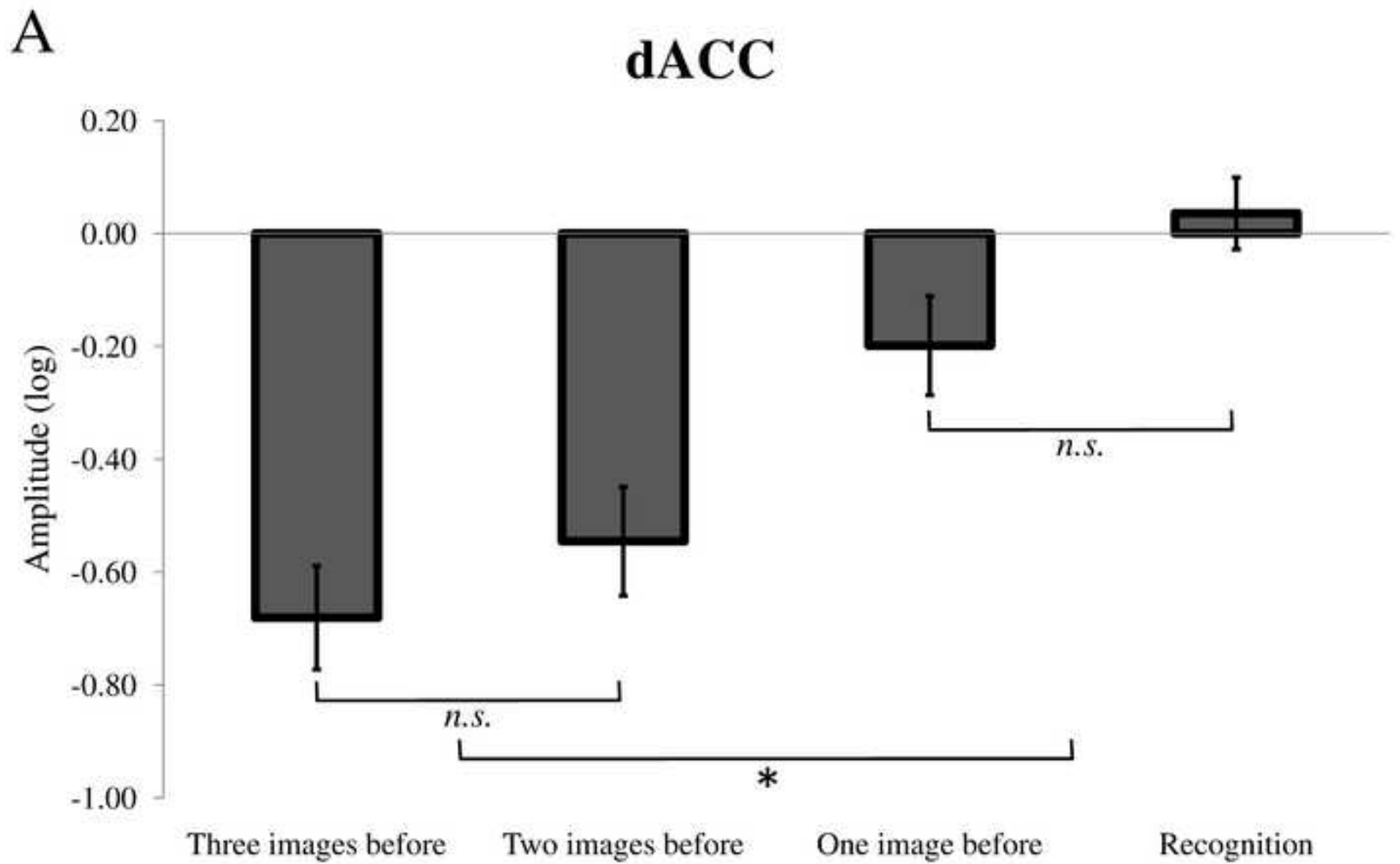


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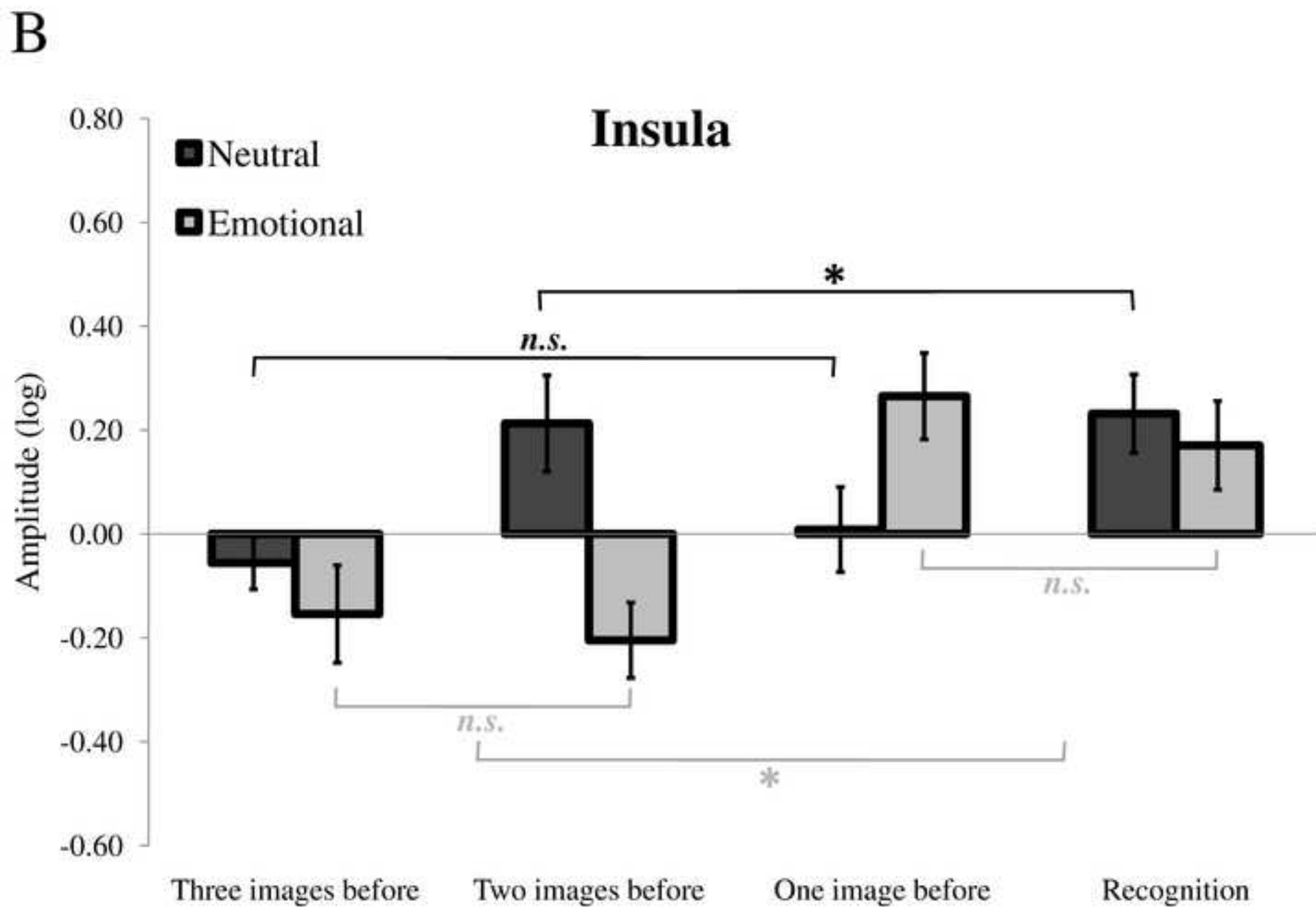


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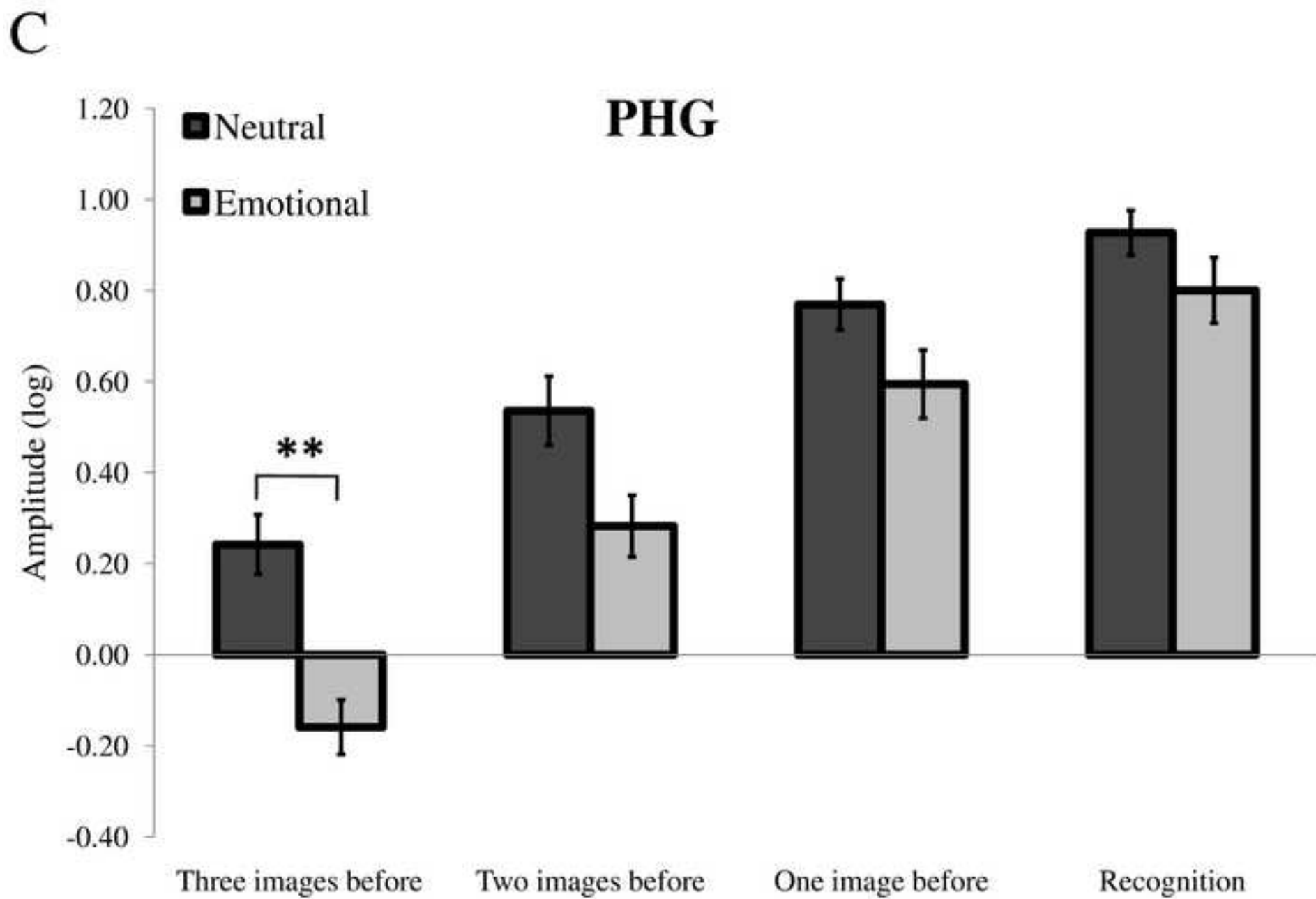


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