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Incongruent object/context relationships in visual scenes: Where are they processed in the brain?

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ABSTRACT

Rapid object visual categorization in briefly flashed natural scenes is influenced by the surrounding context. The neural correlates underlying reduced categorization performance in response to incongruent object/context associations remain unclear and were investigated in the present study using fMRI. Participants were instructed to categorize objects in briefly presented scenes (exposure duration = 100 ms). Half of the scenes consisted of objects pasted in an expected (congruent) context, whereas for the other half, objects were embedded in incongruent contexts. Object categorization was more accurate and faster in congruent relative to incongruent scenes. Moreover, we found that the two types of scenes elicited different patterns of cerebral activation. In particular, the processing of incongruent scenes induced increased activations in the parahippocampal cortex, as well as in the right frontal cortex. This higher activity may indicate additional neural processing of the novel (non experienced) contextual associations that were inherent to the incongruent scenes. Moreover, our results suggest that the locus of object categorization impairment due to contextual incongruence is in the right anterior parahippocampal cortex. Indeed in this region activity was correlated with the reaction time increase observed with incongruent scenes. Representations for associations between objects and their usual context of appearance might be encoded in the right anterior parahippocampal cortex.

1. Introduction

In our everyday environment, objects most often appear in typical visual settings that contain other related objects arranged in specific spatial configurations. This provides us with a rich set of semantic and spatial contextual associations that are implicitly learned through visual experience. Accordingly, the concept of *schemata* has been introduced to describe a high-level unified representation for contextual associations in a scene (Biederman, Mezzanotte, & Rabinowitz, 1982; Hock, Romanski, Galie, & Williams, 1978; Mandler & Johnson, 1976). During the processing of real-world scenes, *schemata* would be activated in a rapid and automatic manner. Following this latter hypothesis, object search and recognition are facilitated when objects are seen in an expected *congruent* context and at an expected position and size (Bar, 2004; Biederman et al., 1982; Chun, 2000; Ganis & Kutas, 2003; Oliva & Torralba, 2007; Palmer, 1975). Conversely, visual *incongruence* between object and its context of presentation (Davenport, 2007; Davenport & Potter, 2004; Fabre-Thorpe, 2011; Fize, Cauchoix, & Fabre-Thorpe, 2011; Joubert, Fize, Rousselet, & Fabre-Thorpe, 2008; Joubert, Rousselet, Fize, & Fabre-Thorpe, 2007; Kret & de Gelder, 2010; Mudrik, Lamy, & Deouell, 2010) or between pairs of objects (Green & Hummel, 2006; Gronau, Neta, & Bar, 2008; Kim & Biederman, 2010) results in decreased performance when processing object, context or global scene. This consistently reported drop of performance suggests that previously unseen, i.e. incongruent, contextual associations influence visual recognition, possibly because representations for these new associations or *schemata* have not been registered through experience. However, the neural correlates underlying this behavior in response to visual incongruence remain to establish. The present functional magnetic resonance imaging (fMRI) study aimed at determining which neural regions evidence differential activity during processing of semantically-incongruent vs. congruent associations between objects and their surrounding, and how activity in these regions contributes to decrease in object categorization performance.

Medial temporal areas previously involved in contextual binding (Chalfonte & Johnson, 1996; Goh et al., 2004; Mitchell, Johnson, Raye, Mather, & D'Esposito, 2000) are candidate areas that may be

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sensitive to novel object/context associations in incongruent scenes. Through visual experience, objects are not encoded individually, but rather in relation to typical settings. It has been shown that these binding operations are made in an automatic way, without any instructions to relate the different elements in a scene (Cohen et al., 1999; Goh et al., 2004). Relational encoding of visual picture elements, such as a person in a house context (Henke, Weber, Kneifel, Wieser, & Buck, 1999), induces greater activity in right hippocampal and parahippocampal regions relative to separate encoding of the same elements. Using an fMRI-adaptation paradigm during passive viewing of natural scenes, the anterior parts of the right parahippocampal cortex (PHC) and of the right hippocampus were specifically activated when participants successively processed sequences of novel object/context associations compared to repeated ones (Goh et al., 2004). Consistently, increased activity in the anterior part of the PHC during retrieval of meaningless patterns has been related to previous encoding of these patterns in nonspatial configurations (Aminoff, Gronau, & Bar, 2007), which suggests that nonspatial familiar associations between items, or between an item and its context, may be encoded in this region. The hippocampus and anterior part of PHC may receive converging information from more posterior parahippocampal regions about the item features and the context in which items are encountered (Diana, Yonelinas, & Ranganath, 2007; Goh et al., 2004; Suzuki & Amaral, 2004). Therefore these medial temporal regions may show differential involvement when processing incongruent vs. congruent object/context associations. In particular, encoding of never-seen incongruent associations may reinforce relational binding operations, resulting in greater activity in medial temporal regions (Cohen et al., 1999).

In imaging studies that have looked at neural processing of semantically-incongruent contextual associations, changes in brain activity in response to incongruence have been investigated in high-level regions of the visual ventral pathway, the lateral occipital complex (LOC) and the parahippocampal place area (PPA) (Gronau et al., 2008; Jenkins, Yang, Goh, Hong, & Park, 2010; Kim & Biederman, 2010), as well as in the prefrontal cortex (Ganis & Kutas, 2003; Gronau et al., 2008; Mudrik et al., 2010). The former occipito-temporal regions are thought to process bottom-up perceptual information from early visual areas, while the latter frontal region may modulate this processing through top-down mechanisms (Bar & Ullman, 1996; Biederman, 1972; Gronau et al., 2008; Palmer, 1975).

Using line-drawings of interacting object pairs, Kim and Biederman (2010) have reported increased activity in the LOC when objects were semantically unrelated vs. related (e.g. a bird on an ear vs. a bird on a birdhouse), suggesting that the LOC may process interactions between objects. Consistently, Gronau et al. (2008) suggested that activity in the LOC may depend on contextual surroundings of objects. In their study, LOC activity differentiated target-object recognition when primed with semantically-related vs. –unrelated objects. Besides, the PPA may mediate contextual associations (Aminoff et al., 2007; Bar & Aminoff, 2003; Bar, Aminoff, & Ishai, 2008; Bar, Aminoff, & Schacter, 2008). Activations in the PPA are increased when participants are presented with isolated objects that have strong associations with a specific context (e.g. a cow or an oven) relative to objects with only weak contextual associations (e.g. a fly or an apple) (Bar & Aminoff, 2003). It was proposed that representations for contextual associations may be stored within the PPA and activated during processing of highly contextual objects. The concept of *context frames* (Bar & Ullman, 1996), which is reminiscent of the concept of *schemata*, was proposed to describe this long-term memory trace for contextual associations. Activation of representations stored in the PPA may be modulated through top-down mechanisms, as described in a model for object recognition in environmental scenes proposed by Bar and colleagues (Bar, 2004). With a rapid grasp of a scene, the processing of low spatial frequency information would allow access to a coarse object shape and activate, in the prefrontal cortex, a large set of all object representations fitting this shape. In parallel, the extraction of the context frame would restrict the activated representations only to possible objects that could be predicted in such context. Object recognition would be achieved with detailed bottom-up high spatial frequency visual information. Consistent with this model, differential activity in the prefrontal region for congruent and incongruent associations has been reported (Ganis & Kutas, 2003; Gronau et al., 2008; Mudrik et al., 2010), which may reflect activation of semantic knowledge on contextual associations. Using pictures of objects embedded in contexts, Mudrik et al. (2010) have shown that this contextual congruence effect in the prefrontal region occurs around 270 ms after scene presentation. However, decrease in object categorization performance due to contextual violations has been observed for motor responses as short as 270 ms post-stimulus, suggesting that scene incongruence may influence bottom-up perceptual object processing before top-down modulation on high-level visual areas takes place (Joubert et al., 2008).

In the present study, real-world scenes with semantically congruent and incongruent object/context associations were briefly (100 ms) presented, and participants were asked to categorize objects as fast as possible. Stimulus exposure duration was shorter than the duration used in previous imaging studies (Ganis & Kutas, 2003; Gronau et al., 2008; Jenkins et al., 2010; Kim & Biederman, 2010; Mudrik et al., 2010) in order to prevent eye movements and increase speed of response, which may mostly rely on bottom-up visual analysis (Fize et al., 2011; Joubert et al., 2008). Moreover, object categorization performance was recorded in each participant, for congruent and incongruent trials. We hypothesized that high-level regions of the ventral pathway would show differential activity for congruent vs. incongruent scenes. In particular, anterior ventral regions previously involved in object/context binding and processing of contextual associations (Aminoff et al., 2007; Goh et al., 2004) may specifically respond to scene incongruence. Moreover, a key objective in our study was to examine correlations between activity and behavioral performance in object categorization. Such correlation analysis was crucial in order to specifically point towards the locus of incongruence processing that would induce the behavioral cost consistently reported in previous studies (Davenport, 2007; Davenport & Potter, 2004; Joubert et al., 2007, 2008; Mudrik et al., 2010).

2. Material and methods

2.1. Participants

Fifteen healthy volunteers (8 females, 11 right-handed, mean age = 23.6 years, range 20–35 years) gave informed consent for their participation. All of them had normal or corrected-to-normal vision. The study was approved by the local Ethics Committee in Lille, France (CPP n°05/79 Nord-Ouest IV).

2.2. Stimuli

Stimuli were horizontal color scenes (768×512 pixels), all drawn from a large set of scenes created in our lab and previously used in psychophysical experiments (Joubert et al., 2008). All scenes contained a foreground object pasted in a background context. Contexts and objects were selected from commercial CD-ROM libraries (Corel Stock Photo Libraries for the contexts, Hemera Photo Objects for the objects). In order to avoid sharp edges when an object was pasted in a context, progressive transparency was applied on the object contour (2 pixels wide). Objects belonged to either "animal" or "non animal" categories, where "non animal" designated manufactured objects. "Animal" objects included wild animals (elephants, bears, lion, deer, etc.), birds, snakes, etc. "Non animal" objects included furniture, vehicles, small household objects, small buildings, etc. Objects were of variable sizes (ranging from 50 × 130 pixels to 400 × 480 pixels), and average object size was equivalent in both categories (43,053 ± 27,697 pixels for "animal" objects, 42,328 ± 37,740 pixels for "non animal" objects, $p = 0.93$). Word frequency of the objects was evaluated using the Lexique French database (Ferrand et al., 2010). Average frequencies were 14.9 ± 2.8 for "animal" objects and 52.6 ± 16.1 for "non animal" objects. The greater average frequency for "non animals" relatively to "animals" ($p = 0.04$) was driven by 5 "non animal" objects (e.g. "car", "glass", "table", "bed", "plane") with extremely high frequencies (>100). Note however that no access to object name is needed to perform the superordinate categorization task used in the present study. Contexts belonged to either "natural" or "man-made" category. "Natural" contexts included various landscapes (fields, desert, forest, mountains, iceberg) and seascapes. "Man-made" contexts included various cityscapes and indoor scenes. Objects and contexts were combined as follows: each object ("animal" or "non animal") was used to create 2 different scenes (congruent and incongruent), and was pasted both in a "natural" and in a "man-made" context. The position of the object in the scene took into account orientation and coherence criteria (support, interposition, scale (Biederman et al., 1982)) with the additional constraint that each object was of identical size in both congruent and incongruent scenes. Thirty "animal" and thirty "non animal" objects were used, resulting in a total of 120 different scenes. This set therefore included 4 different types of scenes, with 30 scenes in each type: (1) "animal" objects pasted in congruent "natural" contexts (**An-C**), (2) "animal" objects pasted in non congruent "man-made" contexts (**An-NC**), (3) "non animal" objects pasted in non congruent "natural" contexts (**NAn-NC**), and (4) "non animal" objects pasted in congruent "man-made" contexts (**NAn-C**). In each scene, object luminance was adjusted relative to local background luminance so that local contrast between object and context was similar in all stimuli. Context and object luminance was equivalent between conditions (average context luminance, An-C: 108.7 ± 6, An-NC: 104.0 ± 18, NAn-C: 100.1 ± 12, NAn-NC: 100.5 ± 13, $p = 0.23$; average object luminance, An-C: 106.4 ± 25, An-NC: 104.9 ± 22, NAn-C: 101.3 ± 22, NAn-NC: 102.6 ± 19, $p = 0.82$). In each condition, mean object eccentricity (defined as the distance between the fixation cross and the centre of the object) was below 17 pixels (<0.4° of visual angle), therefore similar between conditions. Examples of scenes of each type are shown in Fig. 1. Stimuli were projected on a translucent screen placed in the MRI scanner room, at the feet of the participants. Participants saw them through a mirror attached to the head coil. With this setup, stimuli subtended an approximate visual angle of 8.5 × 5.7°, while objects subtended visual angles ranging from 0.5 × 1.3° to 4 × 4.2°.

2.3. Experimental design

In every experimental condition (An-C, An-NC, NAn-NC, NAn-C), stimuli were presented 3 times each, resulting in a total of 90 trials per condition. Participants underwent 3 fMRI runs that lasted 7 mn 30 s each. A run included 120 categorization trials interleaved with 30 fixation trials (trial duration = 3 s). The order of the trials (including fixation trials) was pseudo-randomized for each subject using a genetic algorithm (Wager & Nichols, 2003), which allowed maximizing statistical power to detect differences in fMRI signal between conditions. Therefore, in each subject, a particular sequence of categorization and fixation trials was determined with the algorithm, and stimuli were randomly affected to corresponding categorization trials. One run included approximately 30 trials for each categorization condition (depending on the pseudo-randomized sequence). In a 3-s categorization trial, the stimulus was briefly presented during 100 ms after a temporal jitter (fixation cross) with random duration between 0 and 1400 ms. After stimulus presentation, a fixation cross was shown until the end of the trial, allowing subject's response. The inter-stimulus interval (ISI) therefore varied randomly from 1500 ms to 4300 ms for consecutive categorization trials (and up to 10,300 ms if fixation trials were presented), preventing anticipative strategies for the subject (Fig. 1, lower panel). The short stimulus exposure duration (100 ms) allowed preventing eye movements and obtaining nearly maximal strength of fMRI activation in temporo-occipital regions (Grill-Spector, Kourtzi, & Kanwisher, 2001).

Participants were actively involved in a rapid visual categorization task. They were instructed to respond as accurately and as fast as possible whether the presented stimulus contained an "animal" or a "non animal" object, using a two-button response pad. Participants used both hands to respond and the order of the buttons was counterbalanced between participants. Response accuracy and reaction times were recorded using software developed in-house (VISION, Laboratoire de Neurosciences Fonctionnelles et Pathologies, Lille). Participants were naïve with respect to the goals of the experimental protocol, i.e. modulation of object/context congruence. Prior to fMRI scanning, participants underwent a 5 min training session for the categorization task (using different stimuli, all congruent). This way they could familiarize with the timing of the task (duration and rate of stimulus presentation, variable ISI) and with the two-button response.

2.4. Imaging protocol

MRI scanning was performed on a 1.5 T MRI scanner (Intera Achieva, Philips, Best, The Netherlands) using an 8-element SENSE head coil. The 3 functional runs consisted of 154 whole-brain $T2^*$-weighted echo-planar scans (EPI) (single-shot, TR = 3000 ms, TE = 45 ms, in-plane resolution = 3.75 × 3.75 mm^2, slice thickness = 4 mm, flip angle = 90°, SENSE factor = 1.4, 38 contiguous oblique axial slices parallel to the anterior commissure – posterior commissure line). In each run, the first 4 scans were discarded to allow steady-state magnetization. In addition, a high-resolution anatomical image of each participant was acquired using a 3D sequence (in-plane resolution = 1 × 1 mm^2, slice thickness = 1.6 mm, TR = 8.2 ms, TE = 4 ms, flip angle = 8°, TFE factor = 192, reconstructed in 1 × 1 × 1 mm^3 resolution).

2.5. Data analysis

2.5.1. Image pre-processing

Imaging data were analyzed using the SPM8 software (http://www.fil.ion.ucl.ac.uk, (Friston et al., 1995)). Functional scans were first corrected for differences in every slice acquisition times within a volume, by interpolating time-courses with a sinc function and considering the signal measured in each slice at the acquisition time of the middle slice. To correct for movement during scanning, EPI volumes were realigned to the first volume of the time-series by calculating a 6-parameter rigid-body transformation for every volume and reslicing each volume with sinc interpolation in space. An unwarp correction was also applied to account for EPI image distorsions due to subject movement in the static magnetic field. For each participant, the anatomical scan was normalized to the Montreal Neurological Institute (MNI) T1 template using nonlinear transformations. Normalization parameters were subsequently applied to EPI volumes, which were

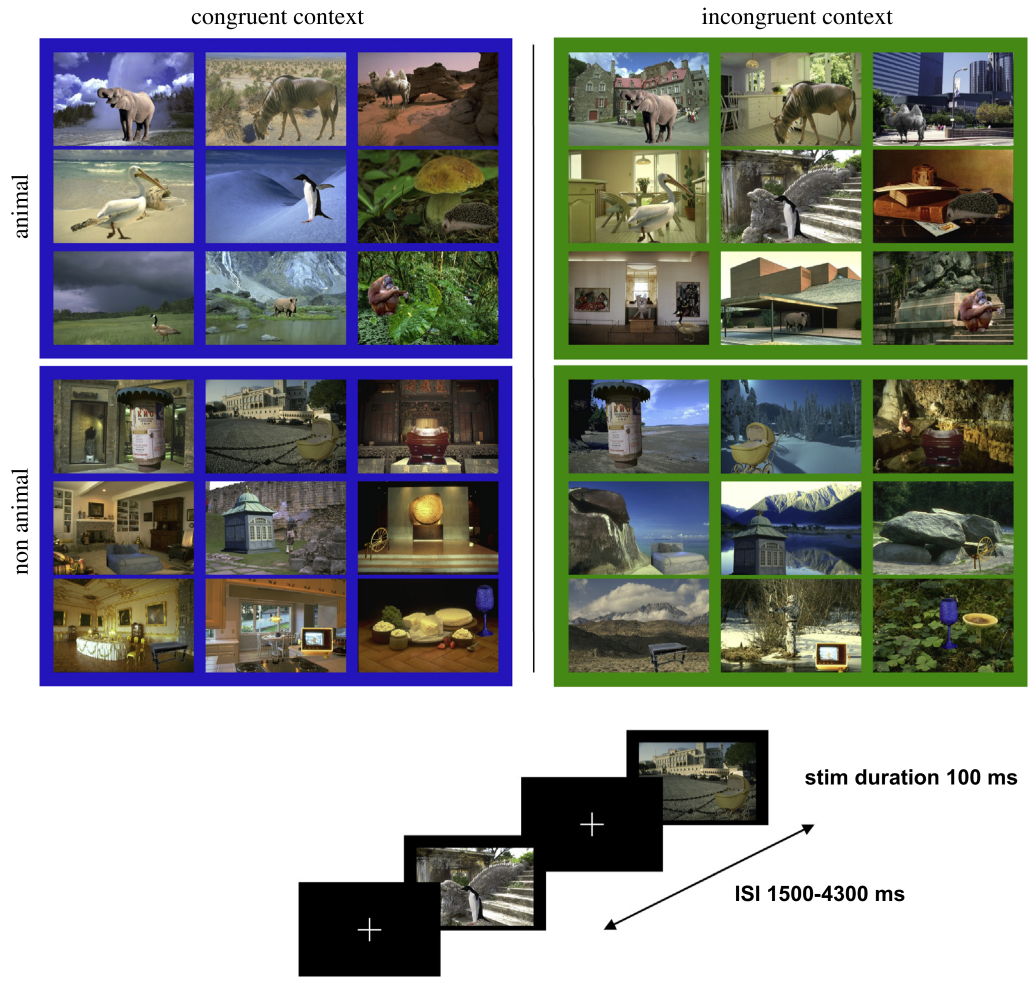

Fig. 1. Examples of stimuli and experimental paradigm. Each object (either "animal" or "non animal") was pasted in both congruent (left upper panel, blue background) and incongruent (right upper panel, green background) contexts. Stimuli were briefly presented (100 ms), with an ISI between 1500 and 4300 ms (lower panel). Each stimulus was presented 3 times during the fMRI experiment. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

re-sampled to $2 \times 2 \times 2$ mm^3 voxels, and smoothed using an 8-mm full-width-at-half-maximum isotropic Gaussian kernel.

2.5.2. Functional data analyses

A within-subject analysis was performed using the general linear model approach (Friston et al., 1995). For every participant, the 3 functional runs were entered in a single design matrix. For each run, 4 event-related regressors representing the different experimental conditions (**An-C**, **An-NC**, **NAn-C**, **NAn-NC**) were used to model the fMRI signal. In these regressors, onsets of stimuli were modeled as delta functions with zero duration, convolved with the canonical hemodynamic response function. Two additional regressors were created with onsets of participant's errors and absences of response to the task, and were included in the model to account for possible extra variance of the fMRI signal, which could be induced by these particular events. Approximately 16% of the trials were modeled in these 2 regressors, with about 14% due to incorrect responding and 2% due to absence of response. Time-courses were high-pass filtered (cut-off = 128 s) and a scaling procedure was applied to account for global signal changes between runs. Contrasts for each of the 4 categorization conditions against rest were computed in every participant.

2.5.2.1. Region-of-interest analysis. Two ROIs in the right anterior PHC and right anterior hippocampus were constrained by 5-mm radius spheres surrounding the coordinates reported by Goh et al. (2004), after transformation of these coordinates from the Talairach to the MNI space (Signed Differential Mapping web project, http://www.sdmproject.com/). The ROI central coordinates used in the present study were (32, −26, −20) for the anterior PHC and (36, −6, −24) for the anterior hippocampus. In both ROIs, parameter estimates of fMRI signal change in the 4 conditions were determined in each subject (averaged on all ROI voxels), using the MarsBar toolbox on SPM8 (Brett, Anton, Valabregue, & Poline, 2002). In each ROI, a 2×2 repeated-measures ANOVA was conducted to examine at group level the main effects of 'congruence' and 'object category' factors, as well as their interaction ($p < 0.05$, Bonferroni-corrected for multiple comparisons).

2.5.2.2. Whole-brain analysis. Significant effects in the group were also examined using a random-effects procedure (Friston, Holmes, Price, Buchel, & Worsley, 1999). Four contrast images per participant (i.e. the 4 categorization conditions vs. rest) were entered in a repeated-measures ANOVA model. Main effects of 'congruence' and 'object category' on brain activations were assessed using ±[(**An-C** + **NAn-C**) − (**An-NC** + **NAn-NC**)] and ±[(**An-C** + **An-NC**) − (**NAnC** + **NAnNC**)] contrasts, respectively. 'Object category' × 'congruence' interactions were assessed using ±[(**An-NC** − **An-C**) − (**NAn-NC** − **NAn-C**)] contrasts, evidencing brain regions where the congruence effect was dependent on object category. For this exploratory analysis, we report all significant activations at a threshold of $p < 0.05$, using FDR-correction for multiple comparisons. Moreover, to further examine patterns of activity across conditions in brain regions evidenced in this whole-brain analysis, parameter estimates of fMRI signal change for each condition were determined in 5-mm radius sphere ROIs centered on peaks of activation clusters (Poldrack, 2007).

2.5.2.3. Stimulus repetition effects. In regions showing differential activity in congruent vs. incongruent conditions (as evidenced from both the ROI and whole-brain analyses), evolution of activations throughout stimulus repetition was examined (as each stimulus was presented 3 times). To this purpose, parameter estimates were computed for the 3 imaging runs separately (corresponding to the 1st, 2nd and 3rd presentations of the stimuli) in each participant, and averaged on all ROI voxels. The effect of stimulus presentation order on brain activity was investigated, as well as its interaction with factor of 'congruence'. Moreover, stimulus repetition effects were further examined at the whole-brain level. To this aim, differences between first and third presentations of stimuli (i.e. between first and third functional runs) were computed for each participant, separately for congruent and incongruent trials. Individual contrast images were then entered in one-sample t-tests to examine group effects of novel vs. repeated scene processing. Both group analyses (for congruent and incongruent scenes) were thresholded at $p < 0.05$, FDR-corrected.

Importantly, stimuli were repeated in our study in order to increase the total number of trials per condition. Identical stimuli were always presented in different imaging runs and at intervals of several minutes. Therefore, our experiment was not designed to investigate effects of stimulus repetition, such as in fMRI adaptation protocols.

2.5.2.4. Relation with behavioral performance. We investigated whether activity in regions differentially involved in congruent and incongruent conditions varied as a function of categorization performance across the 15 participants. In these regions (as evidenced from both the ROI and whole-brain analyses), average parameter estimates of fMRI signal change for each individual were entered in a linear regression model, which included 2 covariates: (1) the decrease in categorization accuracy in incongruent vs. congruent conditions, expressed as a percentage for each individual, and (2) the increase in mean reaction time in incongruent vs. congruent conditions, expressed as a percentage for each individual. To complement this ROI analysis, we further examined the relationship with behavioral performance at the whole-brain level. Individual [(**An-C** + **NAn-C**) – (**An-NC** + **NAn-NC**)] contrasts, i.e. effects of scene congruence in each participant, were entered in a linear regression analysis on SPM8, with the 2 covariates described above. This group analysis was thresholded at $p < 0.05$, FDR-corrected.

3. Results

3.1. Behavioral results

Upon completion of the experiment, all participants reported that they were aware of the incongruence of some of the scenes. Response accuracy and mean reaction time (RT) for correct trials were computed for each participant and each condition, and 2 × 2 repeated-measures ANOVAs were conducted on both variables. Task accuracy was higher for congruent (0.92) relative to incongruent (0.77) trials ($F(1,42) = 52.3$, $p < 10^{-8}$). Moreover accuracy was higher for "non animal" (0.92) vs. "animal" (0.78) objects ($F(1,42) = 57.0$, $p < 10^{-8}$). The interaction between factors of 'congruence' and 'object category' was also significant ($F(1,42) = 13.9$, $p < 0.001$), with the drop of accuracy for incongruent trials being more pronounced for "animal" (from 0.88 to 0.67) vs. "non animal" (from 0.96 to 0.89) objects (Fig. 2). Regarding mean RTs, categorization was significantly faster for congruent (587 ms) vs. incongruent (615 ms) scenes ($F(1,42) = 10.0$, $p < 0.005$). Also participants were faster to categorize "animal" (582 ms) vs. "non animal" (620 ms) objects ($F(1,42) = 18.2$, $p < 0.0005$). The interaction between factors of 'congruence' and 'object category' was not significant ($F(1,42) = 0.01$, $p = 0.91$), showing that the RT increase due to incongruence was equivalent for both object categories (Fig. 2). Note that in the present experiment RTs were globally longer than those recorded by Joubert et al. (2008), which may be explained by different experimental protocols in both studies (i. e. two-button vs. Go–Nogo response, task performance in the MRI environment).

Since "non animal" objects were on average more frequent than "animal" objects (see Section 2), behavioral data were analyzed again after excluding responses to the 5 "non animal" objects with very high frequencies (>100). Following this exclusion, frequencies were equivalent for "animal" (14.9 ± 2.8) and "non animal" (12.8 ± 2.7) objects ($p = 0.63$). Average categorization accuracies for "non animal" objects were 0.96 in congruent contexts and 0.87 in incongruent contexts. Mean accuracy was higher for congruent vs. incongruent scenes ($F(1,42) = 58.7$, $p < 10^{-8}$), and for "non animal" vs. "animal" objects ($F(1,42) = 47.6$, $p < 10^{-7}$). The drop of accuracy due to incongruence was significantly greater for "animal" than "non animal" objects ($F(1,42) = 9.0$, $p < 0.005$). Mean RTs for "non animal" objects were 607 ms in congruent scenes and 635 ms in incongruent scenes. RTs were shorter in response to congruent vs. incongruent scenes ($F(1,42) = 10.1$, $p < 0.005$), and shorter in response to "animal" vs. "non animal" objects ($F(1,42) = 19.7$, $p < 10^{-4}$). This shows that categorization performance was highly similar after equalizing average frequencies of both object categories, and that the use of 5 highly-frequent "non animal" objects did not significantly impact on behavior.

Since each stimulus was presented 3 times during the experiment, we were concerned about a possible impact of stimulus repetition on behavioral results. Therefore, 2 × 2 repeated-measures ANOVAs were conducted for accuracy and RT data calculated on trials corresponding to first presentation of stimuli (30 trials per condition, Fig. S1). Accuracy was higher for congruent vs. incongruent scenes ($F(1,42) = 65.6$, $p < 10^{-9}$) and for "non animal" vs. "animal" objects ($F(1,42) = 64.0$, $p < 10^{-9}$). Moreover, the drop of accuracy due to incongruence was greater for "animal" objects ($F(1,42) = 15.5$, $p < 0.0005$). Mean RTs were shorter for congruent vs. incongruent scenes ($F(1,42) = 9.0$, $p < 0.005$) and for "animal" vs. "non animal" objects ($F(1,42) = 7.3$, $p < 0.01$). Moreover, an additional 2 × 2 × 3 repeated-measures ANOVA was conducted on both accuracy and RT, using within-subjects factors of 'object category', 'congruence' and 'presentation order' (1st, 2nd, 3rd). There were no significant effects for 'presentation order', 'object category' × 'presentation order' interaction, 'congruence' × 'presentation order' interaction, and interaction of the 3 factors for both variables (all Fs < 1.3). These results show that behavioral effects due to scene congruence and object category were observed at first presentation of stimuli, and that the three stimulus repetitions had not significant influence on accuracy or mean RT (Fig. S1).

3.2. fMRI results

3.2.1. Region-of-interest analysis

Group activations in the two right medial temporal ROIs are displayed in Fig. 3. In the right anterior PHC ROI, incongruent conditions induced higher activity than congruent conditions ($F(1,42) = 14.6$, corrected $p < 0.001$). Activity in response to

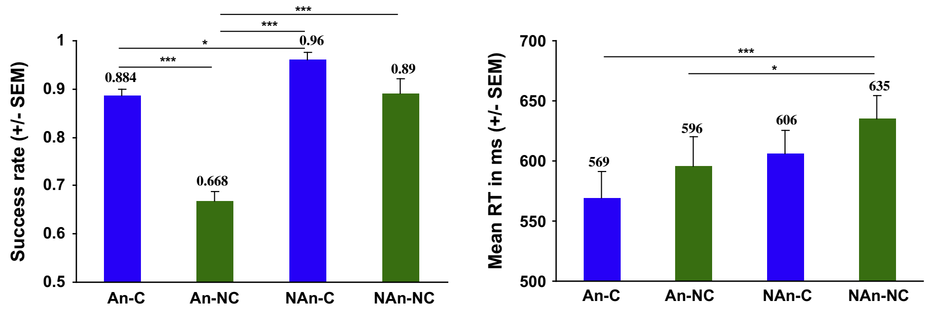

Fig. 2. Behavioral results in the categorization task. Response accuracies (left panel) and mean reaction times (RT, right panel) were averaged across the 15 participants. Congruent conditions are indicated in blue and incongruent conditions are indicated in green. Bar-plots indicate average group performance in the 4 experimental conditions. Error bars indicate s.e.m. in the group. Post hoc Tukey tests were computed to examine significant differences between conditions ($^{*}p < 0.05$; $^{***}p < 0.001$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

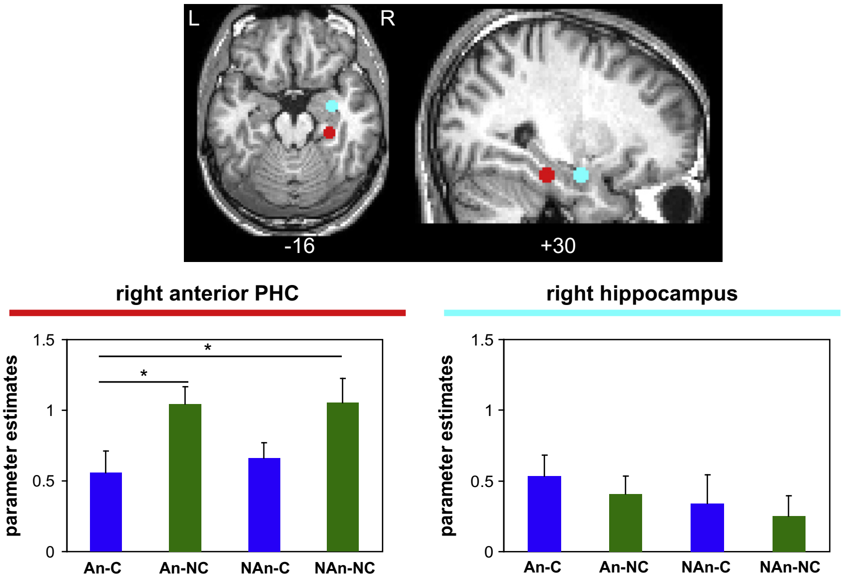

Fig. 3. Patterns of group activity in hypothesized ROIs (right anterior parahippocampal cortex (PHC) and right anterior hippocampus). ROIs are shown on axial and sagittal views of a representative subject's brain. For each ROI, bar-plots show the mean parameter estimates of fMRI signal change for the 4 experimental conditions. Error bars indicate s.e.m. for the group. Post hoc Tukey tests were computed to examine significant differences between conditions ($^{*}p < 0.05$).

"animal" and "non animal" objects was not different ($p = 0.64$), and the increase of activity due to incongruence was equivalent for both object categories ($p = 0.68$). In the right hippocampal ROI, scene congruence and object category did not significantly impact on activity.

3.2.2. Whole-brain analysis

Results of this exploratory analysis are displayed in Fig. 4 and Table 1. Incongruent scenes induced higher activity than congruent ones in the right middle and inferior frontal gyri. The inverse contrast of congruent vs. incongruent scenes did not reveal any regions of activation. The contrast of "animal" vs. "non animal" objects revealed bilateral activation in the posterior fusiform gyri, most likely corresponding to the medial part of the LOC, as well as activation in the posterior visual cortex (BA 17), the left inferior frontal gyrus and cingulate gyrus. Conversely, the contrast of "non animal" vs. "animal" objects did not reveal any significant activations. Finally, the interaction contrast revealed several regions where the increase of activity related to incongruence was more important for "animal" than "non animal" objects (as determined from the patterns shown in Fig. 4). These regions included the posterior part of the parahippocampal gyrus bilaterally, most likely corresponding to the PPA, the right middle occipital gyrus and the posterior visual cortex (BA 17). The inverse interaction contrast did not reveal any significant activation.

3.2.3. Stimulus repetition effects

Repetition effects were investigated in regions evidencing a significant effect of congruence, i.e. the right anterior PHC and the right frontal cortex. Results are shown in Supplementary Fig. S1 (lower panel). In all ROIs, a 2 × 3 repeated-measures ANOVA was conducted on factors of congruence (C, NC) and presentation order (1st, 2nd, 3rd). In each ROI, incongruent scenes induced higher activity than congruent ones (all corrected $p < 0.05$). There was a marginal effect of presentation order in the right middle frontal region (with activity increasing across repetitions, corrected $p < 0.1$) and no effect in right inferior frontal and anterior PHC ($p > 0.3$). Moreover, there were no significant interactions between congruence and presentation order in any of the three ROIs (all $p > 0.4$), showing that repetition of congruent and incongruent stimuli had equal influence on brain activations. Regarding whole-brain analyses of repetition effects, there was not any significant changes in activity between first and third presentations of stimuli, for neither congruent nor incongruent scenes ($p < 0.05$, FDR-corrected).

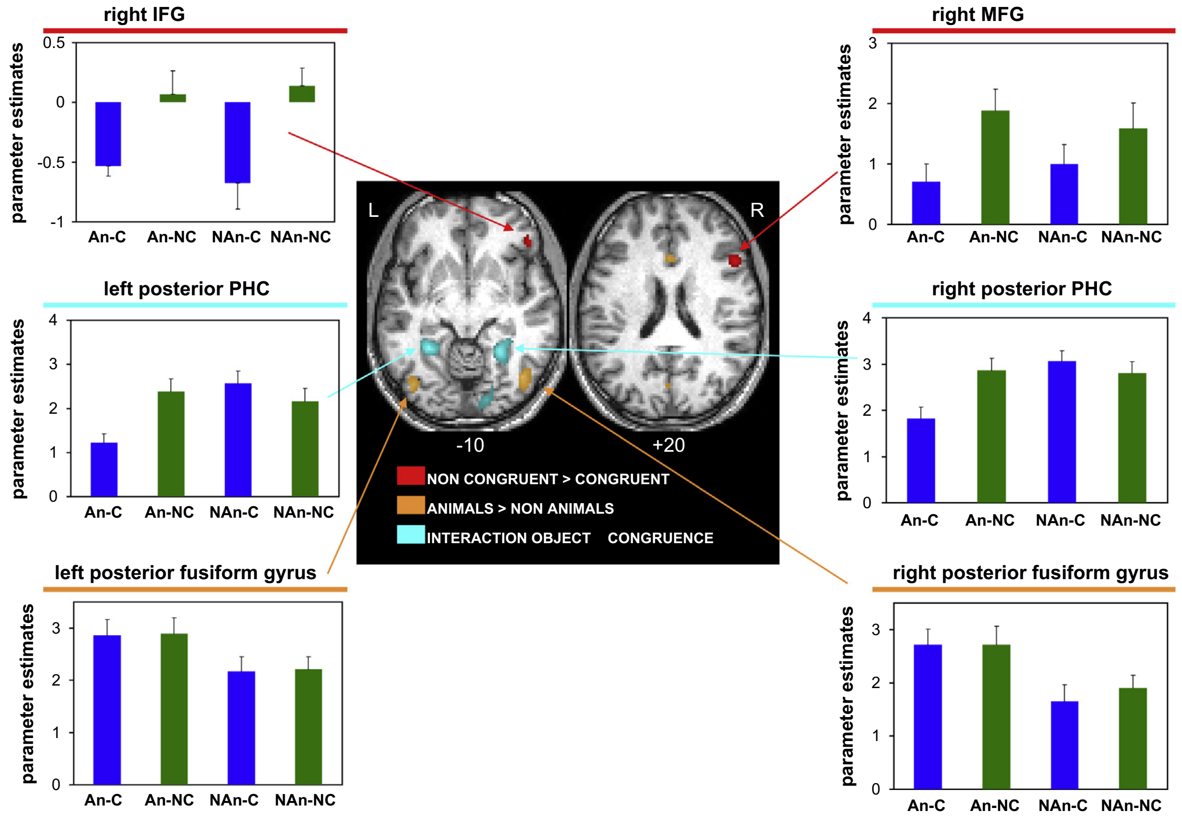

Fig. 4. Group results of the whole-brain analysis. Activations are superimposed on axial views of the normalized anatomical scan of one participant. Views are in neurological orientation (left is left). The MNI z coordinate (in mm) is indicated for each view. SPMs are thresholded at $p < 0.05$ (FDR-corrected). All regions are listed in Table 1, with peak coordinates and t-values. In several regions, ROIs were built as 5-mm radius spheres around peak coordinates (see Section 2). For each ROI, bar-plots show the mean parameter estimates of fMRI signal change for the 4 experimental conditions. Error bars indicate s.e.m. for the group. PHC, parahippocampal cortex. IFG, inferior frontal gyrus. MFG, middle frontal gyrus.

Table 1
Whole-brain analysis.

Brain region	Laterality	Brodmann's area	Peak coordinates			Peak t-value	Cluster-level corrected p	Cluster extent[a]
			x	y	z			
Non congruent > congruent (**An-NC** + **NAn-NC**) > (**An-C** + **NAn-C**)								
Middle frontal gyrus	R	46	52	22	24	4.70	0.008	132
Inferior frontal gyrus	R	47	50	36	−8	4.29	0.045	58
Animals > non animals (**An-C** + **An-NC**) > (**NAn-C** + **NAn-NC**)								
Posterior fusiform gyrus	R	19	46	−74	−4	5.90	<0.001	433
Medial occipital cortex	R/L	17	10	−78	6	5.51	<0.001	568
Posterior fusiform gyrus	L	19	−44	−82	−4	5.38	0.005	226
Inferior frontal gyrus	L	46	−46	34	10	4.18	0.05	45
Anterior cingulate gyrus		24/32	0	24	24	4.03	0.05	62
Interaction (**An-NC** − **An-C**) > (**NAn-NC** − **NAn-C**)								
Parahippocampal gyrus	R	36	26	−50	−10	5.91	0.004	275
Parahippocampal gyrus	L	36	−30	−46	−8	5.91	0.014	215
Middle occipital gyrus	R	19/39	32	−80	10	4.47	0.025	86
Medial occipital cortex	R	17	16	−88	−8	4.35	0.003	297

[a] In $2 \times 2 \times 2$ mm^3 voxels.

3.2.4. Relation with behavioral performance

In our group of 15 participants, decreases in categorization accuracy due to incongruence ranged from 8.4% (from 0.97 to 0.89) to 33.2% (from 0.86 to 0.57), and increases in mean reaction times due to incongruence ranged from 0.5% (from 464 to 467 ms) to 10.1% (from 643 to 708 ms). The impact of scene congruence on categorization performance was thus variable across participants, and the range of individual performance values allows for assessment of a correlation between behavior and neural activity in the group. A linear regression model was used to examine how categorization performance, i.e. decrease in accuracy and increase in mean RT, may relate to the difference in fMRI activity between congruent and incongruent conditions. This regression analysis was done in ROIs showing a significant effect of congruence (i.e. right anterior PHC and right frontal cortex) and at the whole-brain level. In the right anterior PHC region, activity was related with reduction in performance ($r = 0.63$, $p = 0.03$), this relationship being marginal after correction for multiple comparisons ($p = 0.09$). Importantly, the right anterior PHC activity was significantly correlated with percentage of RT increase ($t(14) = 2.83$, corrected $p = 0.045$, t-test on the null hypothesis that the slope of the relation is equal to 0) (Fig. 5). This result suggests that participants who showed the strongest increases of anterior PHC activity due to incongruence evidenced the strongest reduction in categorization performance (in term of speed). In the right inferior and middle frontal cortex, no relationship with behavior was found (corrected $p > 0.9$). The whole-brain analysis did not evidence any additional area where activity was significantly correlated with performance ($p < 0.05$, FDR-corrected).

4. Discussion

This fMRI study aimed at determining the neural correlates underlying the decrease in visual recognition performance induced by scene incongruence, which has been consistently reported in previous studies (Davenport, 2007; Davenport & Potter, 2004; Fize et al., 2011; Joubert et al., 2007, 2008; Mudrik et al., 2010). In the present work, scene incongruence actually resulted in poorer object categorization performance. It has to be noted that different results were found for both object categories. On one hand, participants were faster to categorize "animals", in either congruent or incongruent contexts. In contrast with the vast category of "non animal" man-made objects, all exemplars of the "animal" category share specific structural features. During bottom-up perceptual processing, occipito-temporal regions may be especially responsive to these specific visual patterns (Noppeney, Price, Penny, & Friston, 2006). Consistently, we found that "animal" objects induced higher activity than "non animal" objects in the posterior fusiform gyrus, which is part of the LOC and has shown preferential responses to various semantic categories (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Mechelli, Price, Friston, & Ishai, 2004; Noppeney et al., 2006). Therefore, visual similarities between "animal" exemplars may have resulted in faster responses. On the other hand, categorization performance decrease due to context incongruence was more pronounced for "animal" than "non animal" objects. In particular, accuracy was strongly reduced when "animals" were seen in artificial contexts. This is likely due to strong contextual associations evoked by "animal" objects that were expected in natural landscapes, relative to the large category of man-made objects, for which contextual expectations might vary and might be much less specific (Bar & Aminoff, 2003). However, we cannot exclude the possibility that the larger accuracy drop observed in the incongruent "animal" condition may have been enhanced by our set of stimuli. Man-made contexts consisted in outdoor urban or indoor scenes, which may comprise man-made objects. Although "animal" target-objects were the foreground objects in the scenes, the presence of other man-made objects in the background may have increased the number of errors observed in the An-NC condition. However, our results are consistent with a recent report on categorization of "animals" in incongruent contexts using highly-controlled stimuli (Fize et al., 2011). Moreover the goal of the study was not to compare the effect of incongruence on the two object categories. Rather, our objective was to reproduce the well-known drop of performance in object processing induced by contextual incongruence, as previously reported (Davenport & Potter, 2004; Fize et al., 2011; Joubert et al., 2008), in order to investigate the cerebral structures involved in the processing of object/context incongruent associations and whose activity is linked with behavioral scores.

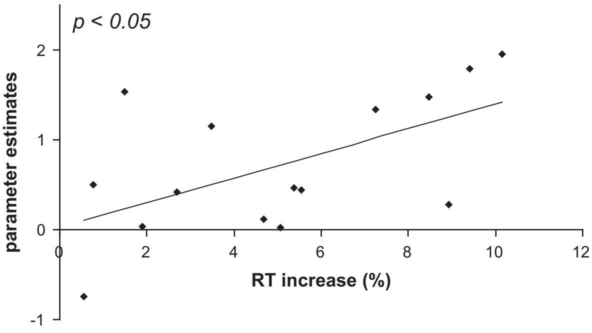

Fig. 5. Correlation between fMRI activity in the right anterior parahippocampal cortex (PHC) and reaction time increase for NC vs. C contrasts, across the 15 participants. The measure of fMRI activity was obtained by averaging parameter estimates of each voxel in the right anterior PHC ROI (Fig. 3) for the [(An-NC + NAn-NC) – (An-C + NAn-C)] contrast, in every participant. The RT increase represents the percentage of increase of the mean RT for incongruent relative to congruent scenes, for every participant.

Where in the brain is the neural source of this robust behavioral effect in response to incongruent scenes? Our fMRI findings showed that activity in one of our hypothesized ROIs, i.e. the right anterior hippocampus, was not influenced by scene incongruence. Conversely, incongruent scenes elicited increased activations in the right anterior PHC, which were observed regardless of object category. In this latter region, a correlation could be evidenced between individual increase of activity and increased reaction times. In addition, based on results of the whole-brain analysis, activity in the right frontal cortex was increased in response to incongruent vs. congruent scenes (for both object categories). Finally, in the posterior part of the PHC, most likely corresponding to the PPA, activity was found to increase in response to incongruent scenes, specifically for "animal" objects.

Several aspects of our categorization task may account for the increased right prefrontal activity when processing incongruent scenes. Activation of the frontal cortex could be due to the detection of semantic incongruence (Ganis & Kutas, 2003; Gronau et al., 2008; Mudrik et al., 2010). As suggested by Mudrik et al. (2010), object identification may be impaired due to the discrepancy between the object semantic representations activated following rapid grasp of the gist of the scene, i.e. the context, and those activated by the visual information from the object actually present in the scene. In their study, an early frontal negativity occurring at 270–600 ms post-stimulus for incongruent vs. congruent scenes was thought to reflect processing of contextual violations (Mudrik et al., 2010). More generally, activation in the right middle and inferior prefrontal gyri has been observed in response to oddball stimuli regardless of their perceptual, semantic or emotional nature (McCarthy, Luby, Gore, & Goldman-Rakic, 1997; Strange, Henson, Friston, & Dolan, 2000). It suggests that this area may have a role in monitoring discrepancies between expected and actual stimuli, and could be part of a generic 'deviance detection system' (Strange et al., 2000). Based on this interpretation, our results in the right prefrontal region point to its possible role in detecting unusual object/context associations (Gronau et al., 2008; Mudrik et al., 2010). However, the lack of correlation between increase of prefrontal activity and decrease of performance suggests that, if this activity reflects processing of semantic contextual violations, this semantic analysis did not contribute to the decrease in performance. Moreover, other aspects of our rapid object categorization task may also account for the increase of prefrontal activity with incongruent scenes. Indeed participants had to solve conflicts of both perceptual and motor nature, when presented with objects in incongruent contexts. In particular, they had to select relevant information, i.e. the foreground object, among competing irrelevant information, i.e. the context. Task preparation for object categorization would involve top-down modulation onto visual areas (Chadick & Gazzaley, 2011) and the frontal cortex could play an important role in enhancing the processing of relevant information while inhibiting the processing of irrelevant one. Such modulation of processing in visual ventral areas would strongly reduce conflicts regardless of their perceptual, semantic or motor nature. Moreover, when faced with incongruent scenes, participants also had to inhibit the competing inappropriate response associated with irrelevant information. Such inhibition processes have been shown to involve the right middle prefrontal cortex (Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Garavan, Ross, & Stein, 1999), which may explain why this region was consistently activated in all participants when processing incongruent scenes.

The activation pattern in the posterior PHC evidenced reduced activity for "animals" in congruent contexts, whereas higher activity was found in the 3 other conditions. This pattern may be explained on the basis of behavioral results. Indeed the accuracy drop induced by object/context incongruence was much more pronounced with "animal" objects (21% drop) than with "non animal" objects (7% drop). Consistently, posterior PHC activation observed for "animal" objects in congruent vs. incongruent contexts was significantly decreased, whereas no differential activity could be evidenced with "non animal" objects. As previously mentioned, the "animal" category likely induced stronger semantic expectations on the specific associated contexts. According to Bar and Aminoff (2003), these associations may be registered in the posterior PHC, i.e. the PPA. In incongruent scenes, the actual stimulus did not match expectations, resulting in activation of competing contextual associations in the PPA as well as categorization errors. An alternative explanation may also be proposed that takes into account a possible bias of our set of stimuli. Indeed, low-level visual features have been shown to affect cerebral activity in extrastriate regions (Cant & Goodale, 2007; Henderson, Larson, & Zhu, 2007). In particular, there is recent evidence that activity in the posterior PHC is sensitive to spatial frequency content of visual stimuli (Andrews, Clarke, Pell, & Hartley, 2009; Rajimehr, Devaney, Bilenko, Young, & Tootell, 2010). Natural objects and contexts intrinsically differ from man-made ones in their spatial frequency content (Torralba & Oliva, 2003) and this low-level parameter was not equivalent between conditions in our experiment. Therefore the pattern of activity observed in the posterior PHC may be induced by a preferential response of this region to the spatial frequencies typically contained in man-made objects and contexts (Henderson et al., 2007). Thus, further investigation is needed to determine the precise impact of stimulus spatial frequency content on posterior PHC activity. Future experiments should use a more elaborate fMRI design, with 4 additional conditions where objects would be pasted on Fourier phase-scrambled versions of contexts (Andrews et al., 2009; Epstein & Ward, 2010). Moreover, the use of two object categories, each of them being strongly associated with specific contexts (Bar & Aminoff, 2003), may help to determine the exact contribution of contextual expectations on posterior PHC activation.

In contrast, the right anterior PHC region showed higher response to incongruent vs. congruent trials, for both object categories. This suggests that this region was responsive to object/context incongruence within our set of stimuli. There is evidence that the anterior PHC region might be involved in the binding of objects with their usual context of presentation through repeated experience (Aminoff et al., 2007). In a previous study (Goh et al., 2004), the successive repetition of scenes (same object and context) induced fMRI-adaptation of the right anterior PHC activity. Such adaptation was not observed when only the context or only the object were repeated. The authors suggested the involvement of this region in contextual binding, a process that would be engaged in an automatic way (Cohen et al., 1999). Through experience, objects are visually bound with particular contexts and representations of these often-seen object/context associations may be stored in the anterior PHC, as previously suggested (Aminoff et al., 2007; Bar & Aminoff, 2003; Bar, Aminoff, & Schacter, 2008; Park & Chun, 2009; Park, Intraub, Yi, Widders, & Chun, 2007). In our study, incongruent scenes may thus elicit activation of representations for contextual associations that would compete with conflicting bottom-up activated representations. This hypothesis is strengthened by the fact that, in our group of participants, a correlation was found between the increase of anterior PHC activity observed in incongruent conditions and the increase in reaction times in response to such incongruent scenes. Such relationship between cerebral activation and drop in performance reinforce the role of the anterior PHC in object/context binding (Goh et al., 2004) and in storing usual, commonly encountered, object/context associations (Aminoff et al., 2007).

In summary, our study provides evidence for a set of right-lateralized regions, which respond differently to congruent and incongruent scenes. These regions include the middle and inferior frontal gyri, and the posterior and anterior parts of the PHC. Consistently, previous studies have suggested that representations for contextual associations met through visual experience could be registered in the PHC (Aminoff et al., 2007; Bar, 2004; Bar & Aminoff, 2003). These long-term representations would be activated when processing our visual environment, thus facilitating object categorization in congruent contexts. In incongruent scenes, additional processing would be required to resolve conflict between competing activated representations. Our results showed that additional processing in the anterior part of the PHC was correlated with the increase in time needed to categorize objects, suggesting that the anterior PHC may be the neural locus for processing the association between an object and its context of appearance (Aminoff et al., 2007; Goh et al., 2004). The PHC receives converging inputs from the dorsal and ventral visual pathways (Blatt, Pandya, & Rosene, 2003; Suzuki & Amaral, 1994). Moreover, a posterior–anterior hierarchical organization of the PHC has been proposed, where spatial associations would be processed in the posterior part, i.e. the PPA, while the anterior part would be involved in the processing of nonspatial associations, such as semantic associations between items (Aminoff et al., 2007). Moreover, the most anterior regions of the visual ventral pathway, such as the anterior PHC, might process the most complex visual features of the scene, such as the relationships between object and context as previously suggested (Goh et al., 2004; Grill-Spector & Malach, 2004). Our present results are in agreement with such proposals, suggesting a hierarchical organization of visual representations in the ventral pathway. Through bottom-up perceptual processing of environmental scenes, corresponding representations, if they exist, may be activated and facilitate perception. Conversely, additional processing will be needed for unusual incoming visual information, resulting in a drop of performance.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandc.2013.10.008.

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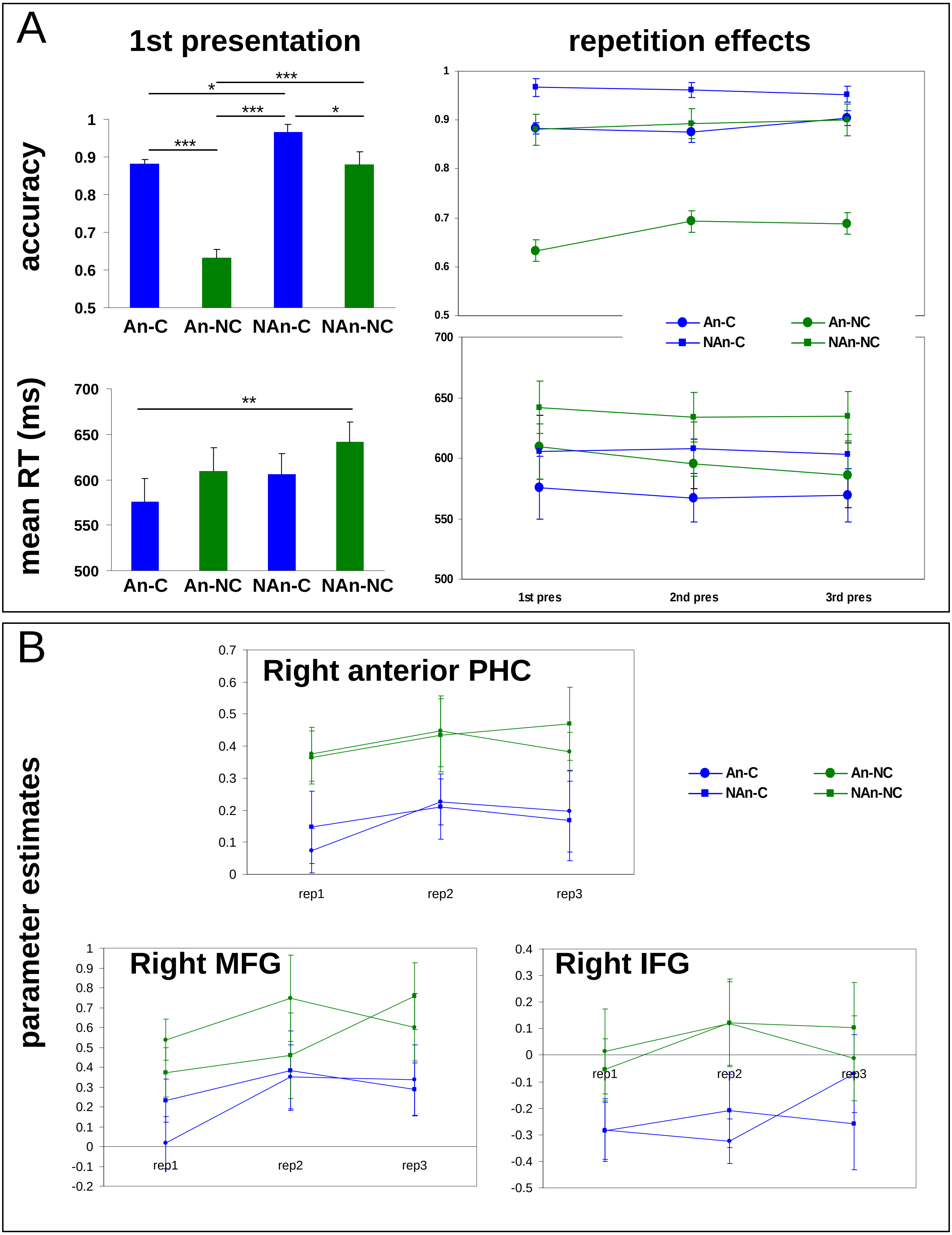
A
1st presentation
repetition effects
accuracy
1
0.9
0.8
0.7
0.6
0.5
***
*
***
*
***
An-C
An-NC
NAn-C
NAn-NC
mean RT (ms)
700
650
600
550
500
**
An-C
An-NC
NAn-C
NAn-NC
An-C
An-NC
NAn-C
NAn-NC
1st pres
2nd pres
3rd pres
B
parameter estimates
Right anterior PHC
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
rep1
rep2
rep3
An-C
An-NC
NAn-C
NAn-NC
Right MFG
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
rep1
rep2
rep3
Right IFG
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
rep1
rep2
rep3