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PRE-PRINT PUBLICATION

AGE EFFECTS ON THE NEURAL PROCESSING OF BRIEFLY FLASHED INCONGRUENT NATURAL SCENES

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Running title: Fast scene processing in older adults

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Abstract

In daily life, fast visual recognition of surrounding objects is facilitated through context-based expectations. However the ability to rapidly and accurately recognize unexpected stimuli in a given environment is also crucial and this ability is impaired with age. The present fMRI study aimed at comparing in young and older adults the neural correlates of fast object processing. Patterns of cerebral activity were investigated in response to briefly-presented (100 ms) congruent and incongruent natural scenes. Participants were slower and less accurate when categorizing objects in incongruent relative to congruent contexts. This behavioral cost was notably more pronounced in the older group. Height and multivariate patterns of fMRI activity in context-selective regions were equivalent in both age groups, suggesting preserved processing of coarse scene features in older participants. Incongruent scenes elicited additional activity in the parahippocampal gyrus that possibly reflected simultaneous activation of rarely co-occurring neural representations. Contextual effects were observed in object-selective cortex for the young group only, and may be driven by detection of mismatch between perceived and previously experienced associations. In the older group exclusively, increased bilateral prefrontal and left fusiform activity in response to incongruent scenes was observed. However this supplemental activity was not found to efficiently contribute to improve task performance in difficult visual conditions. Altogether these results suggest age-related changes in the interaction between object- and context-processing pathways, that may subserve impairment in identification of unexpected objects in natural scenes.

Keywords: healthy aging; fast scene processing; contextual associations; ventral pathway; functional MRI.

1. Introduction

Within very short exposure times such as a few tenths of ms, human observers are able to accurately recognize various objects in a visual complex scene (Biederman, Rabinowitz, J, Glass, A, & Stacy, 1974; Fei-Fei, Iyer, Koch, & Perona, 2007; Greene & Oliva, 2009; Thorpe, Fize, & Marlot, 1996). This impressive ability seems to strongly rely on the use of visual expectations based on our lifelong experience of the surrounding world (Bar & Ullman, 1996; Greene, Botros, Beck, & Fei-Fei, 2015), thus facilitating perception on a daily basis. As a consequence, when scenes deviate from these expectations, i.e. when an object appears in a semantically *incongruent* environment, a deficit in fast object recognition performance is consistently observed (Irving Biederman, Mezzanotte, & Rabinowitz, 1982; Davenport & Potter, 2004; Joubert, Fize, Rousselet, & Fabre-Thorpe, 2008; Mudrik, Lamy, & Deouell, 2010). Longer scene exposure times are needed to reliably report incongruent elements (Greene et al., 2015). We have previously shown that this difficulty in identifying incongruent objects in briefly-presented scenes is increased in older relative to younger adults, whereas rapid processing of congruent objects remains accurate until very old age (Rémy et al., 2013). Imaging results during passive viewing of natural scenes have suggested that older adults' processing of background context would be preserved, whereas processing of salient objects would be diminished (Chee et al., 2006; Goh et al., 2007; Gutchess, Welsh, Boduroğlu, & Park, 2006). Hence the dominant role of gist processing in fast scene perception, as reported in young adults (Greene et al., 2015; Mack, Clarke, Erol, & Bert, 2017), could possibly be emphasized in old age. To our knowledge, age-related differences in the neural substrates of fast visual processing of objects in natural scenes have not been investigated yet. The objective of the present functional magnetic resonance imaging (fMRI) study was to determine, in young and older adults, the neural structures involved in rapid categorization of objects presented in either *congruent* or *incongruent* contexts. In daily life, the ability to detect rapidly and accurately novel or unexpected objects appearing in our visual environment is critical, as a fast appropriate response may be needed. How aging affects this ability, and which aspects of fast visual scene processing undergo age-related changes, are therefore important questions to address.

When presented with brief natural scenes, participants can rapidly categorize either scene context (Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001; Greene & Oliva, 2009; Joubert,

Rousselet, Fabre-Thorpe, & Fize, 2009; Rousselet, Joubert, & Fabre-Thorpe, 2005) or salient objects (Fize, Cauchoux, & Fabre-Thorpe, 2011; Thorpe et al., 1996). If the natural scene includes congruent objects (a polar bear on the floe), strongly interconnected cortical representations, i.e. *schemata* or *context frames* (Bar, 2004; Biederman et al., 1982; Van Kesteren, Ruiter, Fernández, & Henson, 2012), would activate and this would facilitate object identification. Conversely, incongruent scenes (a polar bear in a living room) would activate representations along the ventral stream that have not been repeatedly co-activated through lifelong experience of the surrounding environment. From brief exposure to congruent or incongruent scenes, object and context are processed in parallel along the ventral pathway, and there is behavioral evidence that both processing streams could interfere early, at perceptual stages (Brandman & Peelen, 2017; Fabre-Thorpe, 2011; Mullin & Steeves, 2011). It has been proposed that perceiving incongruent object-context associations could activate conflictual representations in high-level regions of the ventral pathway. The parahippocampal cortex (PHC), including the parahippocampal place area (PPA) in its posterior part, and the fusiform gyrus, which is part of the Lateral Occipital Complex (LOC), are candidate loci where this conflictual processing could occur. Indeed these regions have been involved in object-object or object-context relational processing (Goh et al., 2004; Gronau, Neta, & Bar, 2008; Howard, Kumaran, Ólafsdóttir, & Spiers, 2011; Kim & Biederman, 2011). In particular, the PHC has been proposed to mediate representations for the familiar associations inherent to natural scenes (Aminoff & Tarr, 2015). In a previous fMRI study, increased PHC activity was found in response to incongruent vs. congruent object-context relationships in a group of young adults (Rémy, Vayssière, Pins, Boucart, & Fabre-Thorpe, 2014), and the increase in the anterior part of the PHC was related with the increase in reaction times due to incongruence on a fast object categorization task. This suggests that exposure to previously-unexperienced contextual associations induced additional processing in the PHC that may have contributed to increase the time needed for object processing.

Fast processing of natural scenes and objects is robust with aging. Despite low-level visual deficits, such as reduced acuity, contrast sensitivity or color vision (Owsley, 2011), the ability to rapidly categorize isolated objects or contexts without any salient objects using short exposure times seems well preserved with age (Agnew & Pilz, 2017; Boucart, Despretz, Hladiuk, & Desmettre, 2008; Lenoble, Bordaberry, Rougier, Boucart, & Delord, 2013; Lenoble, Boucart, Rougier,

Bordaberry, & Delord, 2014; Ramanoël, Kauffmann, Cousin, Dojat, & Peyrin, 2015). This indicates that mechanisms involved in rapid gist recognition would be preserved in older adults, although processing of objects embedded in contexts remains challenging when scenes are briefly presented (Rémy et al., 2013). Using longer exposure times to natural stimuli (> 800 ms) that allow for ocular exploration, age-related differences in activity have been consistently demonstrated in high-level regions of the ventral pathway. Functional MRI studies have shown that neural response in ventral regions is less selective to specific categories of stimuli (Burianová, Lee, Grady, & Moscovitch, 2013; Carp, Park, Polk, & Park, 2011; Goh, Suzuki, & Park, 2010; Park et al., 2004; Park et al., 2012). A few studies have explored processing of objects embedded in contexts using either passive viewing or incidental encoding tasks (Chee et al., 2006; Goh et al., 2007; Gutchess et al., 2006; Jenkins, Yang, Goh, Hong, & Park, 2010). Using fMR-Adaptation experiments, neural adaptation in the PPA was found similar in older and young participants, suggesting preserved context processing with age. However, adaptation to repeated objects and to repeated object-context associations was decreased in the LOC and in the anterior PHC respectively for older participants, suggesting reduced object processing. It has been proposed that concurrent visual processing of both object and context is deficient with age due to reduced resources (Chee et al., 2006). Importantly, neural adaptation in the LOC was subject to cultural biases driven by lifelong experience within a given environment, as well as attentional biases related to task instructions, suggesting that scene ocular exploration contributes to these age-related effects. In agreement, natural viewing behavior in older adults was reported to be less driven by stimulus features than by explorative strategies (Açik, Sarwary, Schultze-Kraft, Onat, & König, 2010). Greater influence of explorative strategies with age is consistent with increased frontal recruitment during processing of natural stimuli (Burianová et al., 2013; Grady et al., 1994; Gutchess et al., 2005; Park et al., 2003) and biological motion (Biehl, Andersen, Waiter, & Pilz, 2017), in accordance with a Posterior- Anterior Shift with Aging (PASA) model (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008). However it remains unclear whether a rapid visual task using flashed scenes, which does not permit visual exploration, will induce such age-related differences in ventral and frontal activity.

In the present fMRI study, behavioral performance and brain activity were compared between young and older adults completing a rapid object categorization task with briefly-presented

scenes (100 ms). Such short exposure to stimuli prevented eye movements, while allowing for nearly maximal BOLD response in occipito-temporal regions (Grill-Spector, Kourtzi, & Kanwisher, 2001). Objects were either non-domestic animals or pieces of furniture embedded in either natural outdoor or man-made indoor contexts, resulting in *congruent* or *incongruent* scenes. We first aimed at reproducing the behavioral result of a previous study showing a greater impairment in older participants when categorizing an object in an incongruent context, relative to young participants (Rémy et al., 2013). The main aim was to compare average levels and multivariate patterns of brain activity in response to congruent and incongruent scenes in both groups. We hypothesized that the age-related impairment in fast incongruent object categorization would be explained by differences in activity in object- and scene-selective regions. In particular, PPA activity could stay preserved with age, whereas LOC activity could be altered (Chee et al., 2006; Goh et al., 2007). We also hypothesized increased frontal activity in the older group during fast object categorization, possibly to compensate for altered object processing (Burianová et al., 2013; Gutchess et al., 2005). This increased frontal recruitment may be more pronounced in response to incongruent scenes, due to greater task difficulty.

2. Materials and Methods

2.1. Participants

Forty-eight healthy volunteers from two age groups were recruited for the study. Young participants ($n = 22$, 2 left-handed) were between 19 and 27 years old, and older participants ($n = 26$, 2 left-handed) were between 59 and 77 years old. Three participants were subsequently excluded: two older participants due to neurological abnormalities and one young participant due to excessive movement in the scanner. Information on the remaining 45 participants is given in Table 1. The study was approved by the regional Ethics Committee (CPP Sud-Ouest et Outre-Mer I, ID-RCB 2010-A00775-34) and all participants gave their written informed consent.

All participants underwent detailed neuropsychological assessment, which included tests on daily-life autonomy, global cognitive state, episodic verbal memory, semantic memory, working memory, language, executive functions and speed of processing. Older participants showed reduced speed of processing (digit-symbol test) and reduced free verbal recall performance

(FCSRT) when compared to young participants. All other measures of performance were equivalent between the 2 groups (Table 1).

A basic assessment of low-level vision (with participants wearing correction when needed) was conducted (Table 1). Visual acuity (Armaignac test) was slightly lower in the older vs. young groups ($p = 0.06$) and contrast vision (Pelli-Robson test) was equivalent between groups.

Moreover, color vision was normal in all participants (Ishihara test) and self-reported vision of the Amsler grid was normal in all older participants.

2.2. Stimuli

The set of stimuli used in this study consisted in 400 real-life color pictures, in which a target object was embedded in a context. Object and context pictures were selected from commercial libraries (Hemera Photo Objects and Corel Stock Photo libraries) or from the Internet. Objects were either “animals” (domestic animals were excluded) or “pieces of furniture”. Contexts were either “natural” (seascapes and landscapes without any buildings) or “man-made” (indoor scenes without any foreground objects). The 400 stimuli consisted in 100 sets of 4 stimuli. These sets of 4 stimuli were created by pasting alternatively 2 foreground objects (an animal and a piece of furniture) in 2 contexts (natural and man-made), thereby resulting in 2 *congruent* object-context associations (an animal in a natural outdoor context and a piece of furniture in a man-made indoor context) and 2 *incongruent* object-context associations (an animal in a man-made indoor context and a piece of furniture in a natural outdoor context). Semantic congruence was taken into account when selecting sets of object and context pictures, e.g. a camel was associated with a desert natural context or a penguin was associated with an Arctic natural context to create congruent scenes. Within each set, stimuli were equivalent in contrast and luminance, object sizes were equivalent in number of pixels and objects were placed at identical positions in each of the two contexts, using a home-made software (Fize et al., 2011). Considering all 400 stimuli, and since the study involved a group of old adults, average object size was rather large ($12.7 \pm 4.7\%$ of the image). Examples of sets of 4 stimuli are shown in Fig. 1. Although controlled in terms of low-level visual features, stimuli were representative of daily perception.

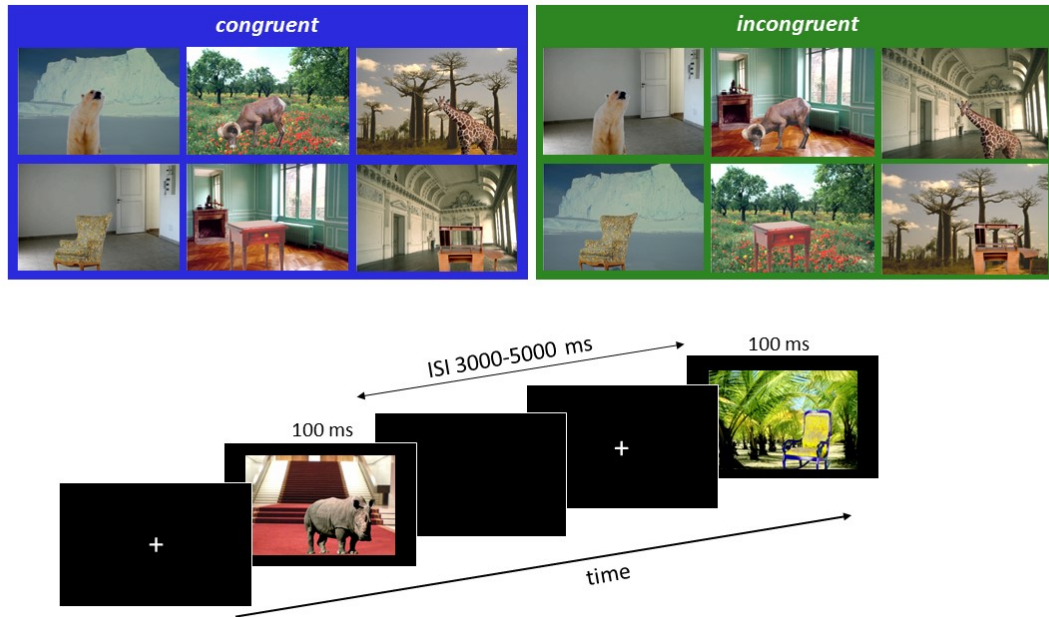


Fig.1. Examples of stimuli and experimental paradigm. Quadrettes were created using a pair of objects (one non domestic animal, one piece of furniture) embedded in a pair of contexts (one natural outdoor, one man-made indoor), resulting in congruent (left upper panel, blue background) and incongruent (right upper panel, green background) scenes. Each stimulus was presented during 100 ms, with an inter-stimulus interval (ISI) between 3000 and 5000 ms (lower panel).

In the scanner room, stimuli were projected on a translucent screen placed at the head of the participants, at an approximate distance of 110 cm. Participants saw them through a mirror attached to the head coil. With this setup, stimuli subtended an approximate visual angle of $9.5^\circ \times 6.3^\circ$, while objects subtended visual angles ranging from $1.4^\circ \times 2.8^\circ$ for the smallest to $8.1^\circ \times 5^\circ$ for the largest. When needed, participants were provided with MRI-compatible glasses with the appropriate visual correction.

2.3. Experimental procedure

2.3.1. Main categorization task

Participants underwent 10 fMRI runs that lasted 3 min 45 s each. Stimuli were presented following a jittered rapid event-related design. A run included 10 null events (fixation cross) and 40 categorization trials (20 trials for the congruent condition and 20 trials for the incongruent condition). The order of the trials was pseudo-randomized for each participant using a genetic algorithm (Wager & Nichols, 2003). In each categorization trial, a central fixation cross was presented randomly between 500 and 1500 ms to prevent anticipatory responses, and was followed by a stimulus briefly presented during 100 ms. The inter-stimulus interval (ISI) varied randomly between 3000 and 5000 ms for consecutive categorization trials, and up to 9000 ms if a null trial was presented.

While in the scanner, participants performed a rapid object categorization task, during which they were asked to press one of two buttons (using two button-pads, one in each hand) as accurately and as fast as possible, depending on whether the stimulus contained an animal or a piece of furniture. The side of the buttons was counterbalanced between participants. All participants were naïve with respect to the goals of the study. Prior to scanning, a 5-min training session with 40 trials for the categorization task was performed (using different congruent stimuli), in order to familiarize participants with the timing of the task and the two-button response.

2.3.2. Passive viewing of objects and scenes

Participants underwent an additional functional run (5 min 45 s) allowing for individual localization of object- and scene-selective brain regions. The run included a total of 16 blocks (duration = 21 s), with 7 stimuli successively presented during 3 s in each block. Four conditions were designed, with 4 blocks in each condition: (1) pictures of isolated objects on a gray background, (2) phase-scrambled versions of these objects, (3) pictures of scenes without any salient objects, and (4) phase-scrambled versions of these scenes. Participants were instructed to attentively look at the different stimuli.

2.4. MRI acquisition and pre-processing

2.4.1. Image acquisition

MRI scanning was performed on a 3T scanner (Achieva, Philips, Best, The Netherlands) of the ToNIC platform (INSERM UMR 1214), using an 8-element SENSE head coil. The 10 functional runs

for the categorization task included successive acquisition of 75 whole-brain T2*-weighted echo-planar (EPI) scans (single-shot, TR = 3000 ms, TE = 35 ms, in-plane resolution = $2.4 \times 2.4 \text{ mm}^2$, slice thickness = 4 mm, flip angle = 90° , 31 contiguous oblique axial slices along the anterior-posterior commissure plane). The localizer run consisted in successive acquisition of 112 whole-brain T2*-weighted volumes with the same acquisition parameters. In each functional run, the first 4 scans were discarded to allow steady-state magnetization. A T1-weighted anatomical scan was also acquired using a 3D sequence (resolution $1 \times 1 \times 1 \text{ mm}^3$, TR = 8.1 ms, TE = 3.7 ms, flip angle = 8° , TFE factor = 240, 160 sagittal slices, acquisition time = 5 min).

2.4.2. Image pre-processing

Imaging data were pre-processed and analyzed using the SPM8 software (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>) (Friston et al., 1995). All EPI volumes were realigned to the first volume using 6-parameter rigid-body transformations. An unwarping procedure (based on a phase map acquired at the beginning of the imaging session) was used to correct for image distortion due to head motion. Individual anatomical and functional images were co-registered and functional images were corrected for slice acquisition timing. A DARTEL procedure was conducted to create a study-specific template (Ashburner, 2007). Each participant's anatomical scan was segmented based on tissue probability maps of grey matter, white matter and CSF in the MNI space provided with SPM. Individual masks of grey and white matter were computed and optimally aligned using nonlinear registration (6 iterations). A study-specific template was created from aligned masks and the template was normalized to the MNI space using linear and nonlinear transformations. For each participant, template normalization parameters and individual deformation fields derived from the segmentation step were then applied to individual anatomical scans and EPI scans acquired during the 10 categorization runs (with re-sampling to $2 \times 2 \times 2 \text{ mm}^3$ voxels). Finally, all EPI volumes were spatially smoothed using a 6-mm full-width-at-half-maximum isotropic Gaussian kernel.

Head motion was compared between age groups, considering absolute values of translations and rotations in each participant. Group values for the 3 translation parameters (young: 0.47 ± 0.24 mm; older: 0.59 ± 0.28 mm) and the 3 rotation parameters (young: 0.009 ± 0.005 degrees ; older: 0.012 ± 0.007 degrees) were not different between groups (both p -values > 0.1).

2.5. Statistical analyses

2.5.1. Behavioral data

Accuracy and mean reaction times (RTs) on correct trials were determined for each participant, in congruent and incongruent conditions. In every individual, the effect of scene incongruence on reaction times was calculated as the percentage of increase in mean RT in the incongruent condition relative to the congruent condition. Note that this latter measure evaluates behavioral cost on RTs due to processing of incongruence, while accounting for general slowing due to age. Accuracies and mean RTs were compared between conditions and groups using mixed 2-way ANOVAs. Percentages of RT increase were compared between groups using a two-sample independent *t*-test. Analyses were performed using the R software (<https://www.r-project.org/>).

2.5.2. Imaging data

2.5.2.1. First-level analyses

For individual analyses of the categorization task, correct trials in each condition were modeled as delta functions with the corresponding temporal onset and zero duration, convolved with the canonical hemodynamic response function (hrf). For each condition, correct RTs were included as a parametric modulator of no interest on a trial-by-trial basis, in order to control for variation of brain activity associated with response latency. Also, onsets of incorrect trials were modeled separately as a regressor of no interest (delta functions of zero duration, convolved with the hrf). Moreover 6 movement parameters (3 translations and 3 rotations) derived from the realignment procedure were included as additional regressors of no interest. A high-pass filter (cut-off period = 128 s) was implemented and a scaling procedure was applied to account for mean signal changes between runs.

2.5.2.2. Region-of-Interest analyses

Individual functional ROIs responding to objects and scenes were determined in each participant's native space. Univariate and multivariate analyses were then performed within each of these ROIs. For univariate analyses, task-related levels of activity were evaluated using the MarsBaR toolbox (<http://marsbar.sourceforge.net/>). Moreover, classification accuracies were determined

using the CoSMoMVPA toolbox (Oosterhof, Connolly, & Haxby, 2016). LDA classifiers were used to discriminate activity patterns in response to animal vs. furniture objects and natural outdoor vs. man-made indoor contexts, within each of the congruent and incongruent conditions. A third LDA classifier was used to discriminate congruent vs. incongruent scenes.

2.5.2.2.1. Individual ROI definition

Functional images from the localizer run were slice-timing corrected, realigned, co-registered to the anatomical image and smoothed (see paragraph 2.4.2.). The 4 conditions (intact objects and scenes, scrambled objects and scenes) were modeled as box-car functions convolved with the hrf, and a high-pass filter (128 s) was applied. Scene-selective regions were obtained from the subtraction contrast of intact vs. scrambled scenes. Each participant's left and right PPA, RSC and OPA were identified from activity clusters found in the parahippocampal cortex, retrosplenial cortex and transverse occipital sulcus respectively, using an uncorrected height threshold of $p < 0.001$ and an extent threshold of 20 voxels. A similar procedure was used to build individual left and right LOC ROIs. Object-selective regions were obtained from the contrast of intact vs. scrambled isolated objects, and LOC activations were identified from clusters found in the lateral occipital cortex and fusiform gyrus. When bilateral activity clusters were found in scene- and object-selective regions, unilateral ROIs were combined as a single functional bilateral ROI. Functional data from the main categorization task were analyzed within each individual ROI. For univariate analyses, the average BOLD response was computed on all ROI voxels. For multivariate analyses and for ROIs larger than 100 voxels, the most significant 100 voxels in each ROI were selected as features.

2.5.2.2.2. Univariate ROI analysis

For univariate ROI analyses, we used functional images corrected for slice acquisition timing and head motion, coregistered to the anatomical image and smoothed, i.e. data were not normalized to MNI space. A GLM model including the 10 categorization runs was estimated, and simple contrasts for Congruent trials vs. baseline and Incongruent trials vs. baseline were computed in every participant. Weighted parameter estimates (beta values) averaged on all ROI voxels were extracted for each contrast of interest. Age and congruence effects were examined within each ROI independently, using 2-way repeated-measures ANOVAs with factors of 'Age' (between-subjects) and 'Congruence' (within-subjects).

2.5.2.2.3. Multivariate ROI analysis

In each participant, GLM models were specified (as described in section 2.5.2.1) for the 10 categorization runs separately. These models were estimated on realigned, slice-time corrected, linearly detrended and smoothed functional images of each run in order to compute beta estimates for each condition and each run. Three LDA classifiers were implemented using a leave-one-out cross-validation procedure. Two classifiers discriminated between animals and pieces of furniture (and between natural outdoor and man-made indoor contexts) within each of the congruent and incongruent conditions. A third classifier discriminated between congruent and incongruent scenes, independently of object and context categories. Classification accuracies were computed in each ROI and for each participant. Age and congruence effects on classification accuracy were then examined using 2-way repeated-measures ANOVAs, as performed for the univariate analysis.

2.5.2.3. Second-level whole-brain analysis

2.5.2.3.1. Univariate whole-brain analysis

Individual contrast images for the categorization task were entered in a random effects model, using the flexible factorial design tool on SPM and following the guidelines from Gläscher & Gitelman for contrast specification (Gläscher & Gitelman, 2008). A 2×2 mixed ANOVA model was implemented, with between-subject factor 'Age' and within-subject factor 'Congruence'. This ANOVA allowed investigating activity specific to incongruence processing (in all participants and within each age group) and age-related differential effects on scene incongruence processing. For every comparison, whole-brain cluster statistics were corrected for multiple comparisons using threshold-free cluster enhancement (TFCE, $p < 0.05$ with 5000 random permutations). Since areas showing significant Age × Congruence interaction were susceptible to explain specific age-related impairment in performance, correlations between object categorization performance and fMRI activity were investigated at local peaks in each of these areas.

2.5.2.3.2. Multivariate whole-brain analysis

A searchlight approach (Kriegeskorte, Goebel, & Bandettini, 2006) was used to implement MVPA at the whole-brain level. In each participant and for each of the classifiers (i.e. decoding object and context category in congruent scenes, decoding object and context category in incongruent scenes and decoding congruent and incongruent scenes), whole-brain classification accuracy

maps were computed using searchlight spheres with a radius of 3 voxels. Individual whole-brain maps were then transformed to MNI space using the individual flow fields previously computed in the DARTEL procedure. Group analyses included (i) nonparametric one-sample t-tests across all participants and within each group, testing for scene congruence decoding accuracy against chance level (0.5), (ii) nonparametric two-sample paired t-tests across all participants and within each group, testing for higher object and context decoding accuracy in congruent relative to incongruent scenes, and (iii) nonparametric two-sample independent t-test comparing congruence decoding accuracies between age groups. In all these tests, cluster statistics on accuracy maps were corrected for multiple comparisons using TFCE ($p < 0.05$, 5000 permutations).

3. Results

3.1. Behavioral results

Group results for accuracy and RT on the categorization task are shown on Fig. 2. Global accuracy varied from 85.7% to 99% in the young group, and from 81.5% to 98.8% in the older group. Young and older participants' accuracies were equivalent ($F(1,43) = 1.38$, $p = 0.25$). Also accuracy was decreased in the incongruent relative to congruent condition ($F(1,43) = 40.95$, $p < 10^{-7}$) and this decrease related to incongruence was more pronounced in the older group (Age \times Congruence interaction, $F(1,43) = 8.17$, $p < 0.007$).

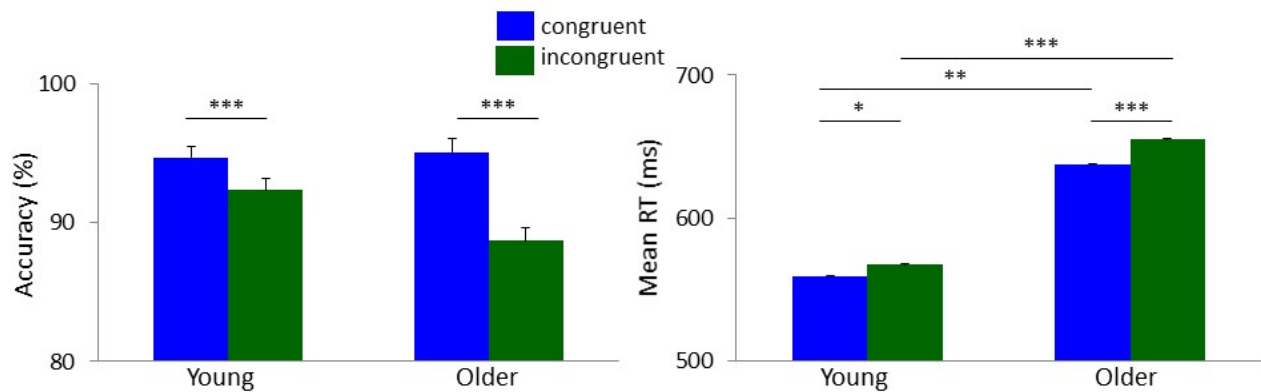


Fig. 2. Behavioral results on the fast object categorization task. Bar-plots indicate average performance in each group, for both experimental conditions. Error bars are s.e.m. in the group. Post-hoc tests were computed to examine significant differences between conditions or groups ($p < 0.01$; ** $p < 0.005$; *** $p < 0.001$).*

Mean RTs varied from 498ms to 663ms in the young group, and from 533ms to 834ms in the older group. RTs were longer in older relative to young participants ($F(1,43) = 17.57, p < 0.0002$). RTs were also longer for the incongruent vs. congruent condition ($F(1,43) = 57.21, p < 10^{-8}$). Increase of RT due to incongruence was more pronounced in the older group (Age \times Congruence interaction, $F(1,43) = 7.15, p < 0.02$). Besides, the average percentage of RT increase due to incongruence was slightly higher in the older group ($t(43) = 2.16, p < 0.04$; young group mean = $1.5\% \pm 1.9\%$, older group mean = $2.74\% \pm 1.96\%$), showing that the larger intra-subject increase of RT in the older group was not fully explained by age-related general slowing on the categorization task.

3.2. Imaging results

3.2.1. Age and congruence effects in object- and scene-selective functional ROIs

When examining localizer data at a threshold of $p < 0.001$ (cluster extent 20 voxels), the LOC ROI was not identified in one older participant, the OPA was not identified in one young and five older participants, and the RSC was not identified in four young and eight older participants.

Task-related activity and object (animal/furniture) or context (outdoor natural/indoor man-made) classification accuracies in object- and scene-selective ROIs for both groups are shown on Fig. 3. In the LOC, equivalent levels of activity were found across groups and conditions. There was no effect of age, congruence or any age \times congruence interaction on LOC activity (all p -values > 0.6). When discriminating congruent from incongruent scenes, classification accuracies in the LOC were above chance in the young group (mean \pm s.d. = $0.56 \pm 0.03, p < 0.01$) and at chance level in the older group (0.52 ± 0.09). The difference in accuracies between groups was significant ($t(42) = 2.6, p < 0.02$). When discriminating objects in congruent and incongruent scenes, classification

accuracies were above chance in all groups and conditions and were equivalent between conditions and groups (all p -values > 0.3) (Fig. 3, right panel).

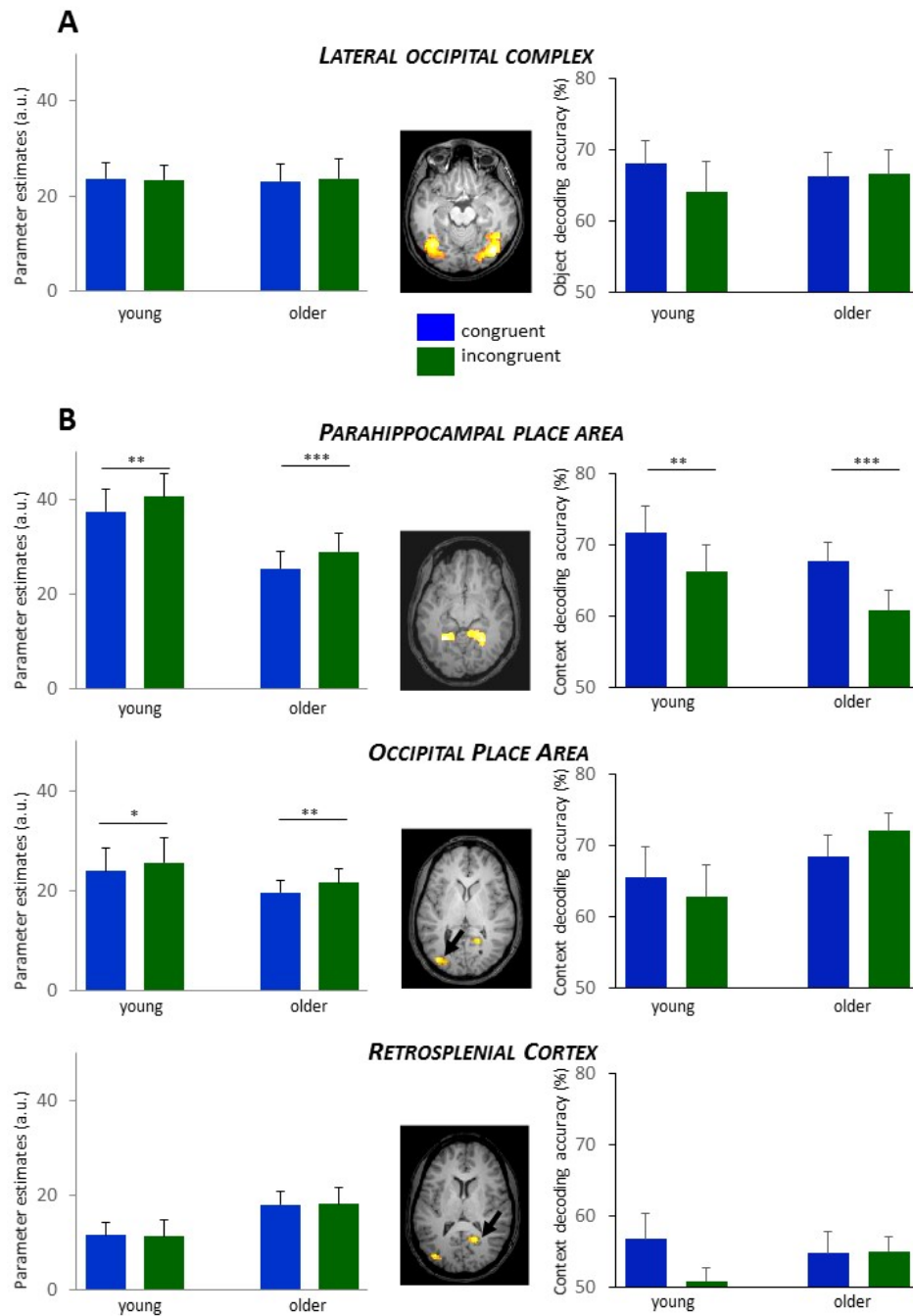


Fig. 3. BOLD response and decoding accuracy in (A) object- and (B) scene-selective regions. Locations of lateral occipital complex (LOC), parahippocampal place area (PPA), occipital place area (OPA) and retrosplenial cortex (RSC) were determined in each participant using a functional localizer (see Methods). Middle panel shows fMRI activity during the localizer run in a

representative older participant (uncorrected $p < 0.001$, extent threshold of 20 voxels). Activations are superimposed on individual anatomical image in native space. In every functional ROI, left panel shows bar-plots for average ROI beta parameter estimates in each group (Young, Older) for each condition (Congruent vs. baseline, Incongruent vs. baseline). Right panel shows bar-plots for average object (animal vs. furniture) and context (natural outdoor vs. man-made indoor) decoding accuracy in each group and condition (chance level at 50%). Error bars are s.e.m. in the group ($p < 0.05$; ** $p < 0.01$).*

Regarding scene-selective cortex, PPA activity was significantly increased in incongruent vs. congruent condition ($F(1,39) = 8.97$, $p < 0.005$). This increase of PPA activity related to incongruence was observed in both young and older participants ($p < 0.005$ and $p < 0.001$ respectively) (Fig. 3, left panel). PPA activity was lower in the older relative to young group, although this age difference was not statistically significant ($p < 0.1$). Accuracies for classification between congruent and incongruent scenes in the PPA were at chance level in both groups (young: 0.52 ± 0.05 , older: 0.53 ± 0.08). Accuracies for context classification were above chance in all conditions and groups. Moreover in both groups, accuracies to discriminate natural and man-made contexts were significantly lower when incongruent objects were present in the scene (main effect of congruence: $F(1,39) = 8.35$, $p < 0.007$; post-hoc tests, young: $p < 0.005$, older: $p < 0.001$) (Fig. 3, right panel). There was neither effect of age nor any age \times congruence interaction on context classification accuracies (all p -values > 0.2).

In the OPA, the BOLD response was significantly increased in incongruent vs. congruent conditions ($F(1,38) = 9.09$, $p < 0.005$), and this increase was found in both groups (young: $p < 0.01$, older: $p < 0.005$) (Fig. 3, left panel). No differences were observed between groups (p -values > 0.4). Classification between congruent and incongruent scenes was at chance in both groups (young: 0.51 ± 0.04 , older: 0.5 ± 0.08). Context classification accuracies were above chance level in both conditions and both groups, and were equivalent across conditions and groups (all p -values > 0.2) (Fig. 3, right panel).

Finally in the RSC, the univariate BOLD response to scenes was similar across conditions and groups (all p -values > 0.2) (Fig. 3, left panel). Classification between congruent and incongruent scenes was at chance level (young: 0.51 ± 0.07 , older: 0.53 ± 0.1). Classification between natural

and man-made contexts was above chance level, except when young participants processed incongruent scenes. There was not any effects of age, scene congruence or age \times congruence interaction on classification accuracies (all p -values > 0.2).

3.2.2. Whole-brain congruence effects

Whole-brain differences between responses to congruent and incongruent scenes were assessed on all participants ($n = 45$, Fig. 4, Table 2). As revealed in univariate analysis, incongruent scenes elicited a higher BOLD response in bilateral PHC, left orbitofrontal cortex and right anterior hippocampus, relative to congruent scenes (TFCE $p < 0.05$, Fig. 4 left panel). The reverse comparison, i.e. congruent vs. incongruent scenes, did not evidence any brain region. Whole-brain searchlight analysis of decoding accuracy showed that object and context decoding in congruent scenes was above chance level in the middle occipital cortex, the parahippocampal and posterior fusiform gyri, and bilateral motor regions (the latter result in motor areas being likely related to participants' motor responses in the object categorization task) (TFCE $p < 0.05$, Fig. 4 right panel, red color scale). Object and context classification was also more accurate in congruent compared to incongruent scenes in the bilateral PHC extending to hippocampus (Fig. 4 right panel, yellow color scale). Moreover classification between congruent and incongruent scenes was significantly above chance in the left fusiform gyrus (vicinity of the collateral sulcus, peak at $(-26, -50, -8)$, peak accuracy = 0.61 ± 0.06) and the right middle frontal gyrus (peak at $(36, 18, 30)$, peak accuracy = 0.58 ± 0.07) (Fig. 4 right panel, blue color scale). As underlined in Fig. 4, there was partial overlap between fusiform regions coding for scene congruence and those coding for object and context in congruent scenes.

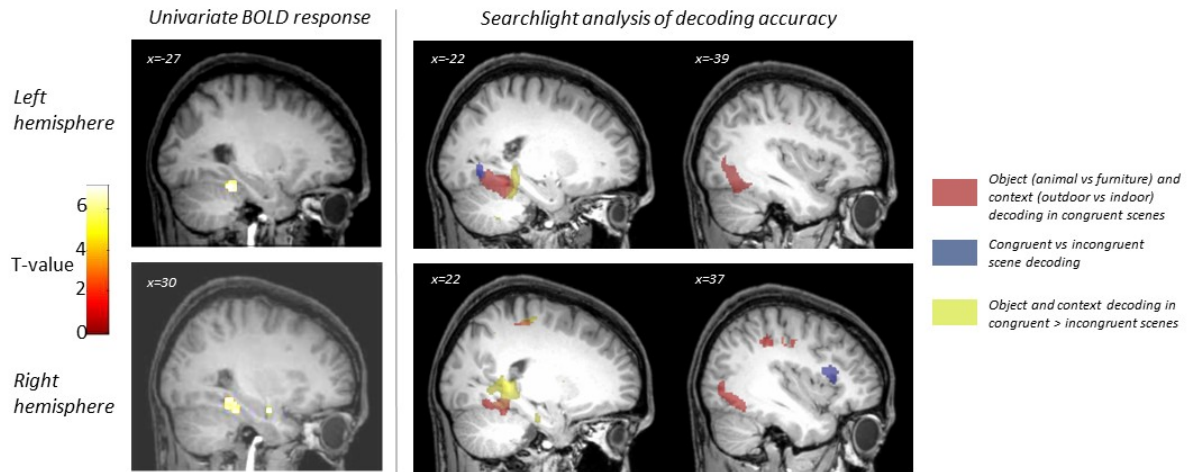


Fig. 4. Scene congruence effects across all participants ($n = 45$). Left panel shows increased univariate BOLD response to incongruent vs. congruent scenes in the bilateral PHC (TFCE, $p < 0.05$). Right panel displays regions evidencing object and context decoding accuracies in congruent scenes above chance level (red), scene congruence decoding accuracies above chance level (blue) and higher object and context decoding accuracies for congruent relative to incongruent scenes (yellow) (TFCE, $p < 0.05$ for all maps). Whole-brain group results are superimposed on an individual anatomical image normalized to MNI space. MNI x coordinate is indicated for each slice.

3.2.3. Within-group whole-brain congruence effects

In the young group, univariate BOLD response was higher for congruent than incongruent scenes in the right posterior insula extending to superior temporal gyrus and in the right parietal cortex, whereas incongruent scenes induced higher activity in the right anterior hippocampus (Suppl. Fig. 1, Table 3). In older participants, incongruent scenes elicited large-extent increased BOLD response in the bilateral fusiform and parahippocampal gyri, in the bilateral middle and inferior frontal gyri, and in the right superior occipital gyrus extending to inferior parietal lobe, whereas no regions induced higher BOLD response for congruent scenes (Suppl. Fig. 1, Table 3). The searchlight analysis of object and context decoding in congruent scenes revealed highly similar results in young and older groups (Suppl. Fig. 1 right panel, red color scale), with accurate decoding in middle occipital, fusiform and parahippocampal gyri, posterior insula and motor

cortex. Object and context decoding were more accurate for congruent vs. incongruent scenes in the bilateral parahippocampal gyrus in both groups, and in the right transverse occipital sulcus, anterior PHC and hippocampus in the young group (Suppl. Fig. 1 right panel, yellow color scale). Finally scene congruence decoding was above chance in the middle frontal gyrus, middle fusiform gyri (vicinity of the collateral sulcus) and right posterior insula in the young group (Suppl. Fig. 1 right panel, blue color scale).

3.2.4. Whole-brain Age \times Congruence interaction effects

The univariate analysis revealed regions with a more pronounced activity increase due to incongruence in older relative to young participants. These regions were the left and right middle frontal gyri and middle fusiform gyri (Fig. 5 left panel, Table 4). Conversely, an activity increase due to incongruence was found in young participants exclusively in the pons. Since differential univariate responses to incongruence were observed in both age groups, we examined in these regions whether activity was related with behavioral performance. In the older group, left fusiform activity in response to incongruent scenes was negatively correlated with categorization accuracy ($r = -0.43$, corrected $p = 0.03$, Fig. 5 left panel). No other significant correlations were found in regions evidencing univariate Age \times Congruence interaction. Multivariate scene congruence decoding accuracies were also compared between groups using searchlight whole-brain analysis. Congruence decoding was more accurate for young participants in the middle occipital cortex (peak at (42,-64,-10), young: 0.57 ± 0.06 , older: 0.48 ± 0.07), the right temporal pole (peak at 44, 10,-12), young: 0.56 ± 0.05 , older: 0.47 ± 0.08) and the right middle frontal gyrus (peak at (38,24,24), young: 0.62 ± 0.04 , older: 0.53 ± 0.09) (Fig. 5 right panel, light blue color scale). Conversely decoding was more accurate for older participants in the left anterior fusiform gyrus (peak at (-40,-52,-6), young: 0.47 ± 0.05 , older: 0.56 ± 0.06) (Fig. 5 right panel, purple color scale).

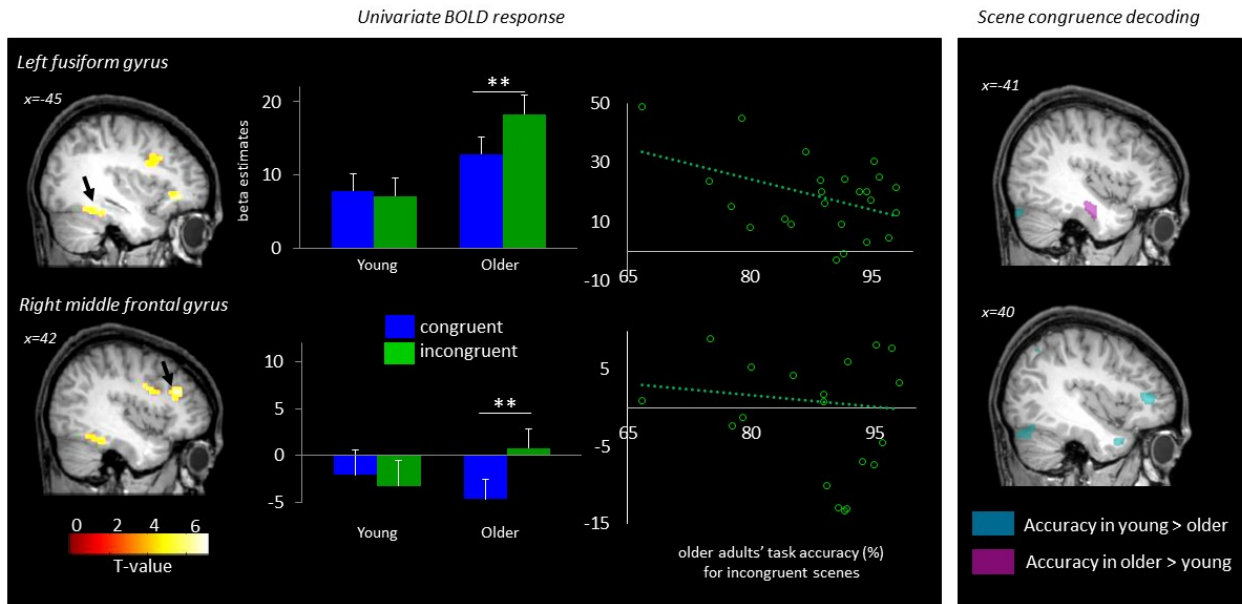


Fig. 5. Regions evidencing significant Age \times Congruence interaction and relation with behavioral performance. The left part of the figure shows interaction results of the univariate analysis. SPMs show regions evidencing differential effects of scene congruence in the two age groups. Bar-plots for average beta estimates in each group and each condition are shown for local peaks of the regions evidenced in the interaction contrast. Error bars are s.e.m. (** $p < 0.005$; *** $p < 0.001$). Correlations between individual accuracy on the categorization task and local peak activity height within older participants for the incongruent condition are displayed. The right part of the figure shows scene congruence decoding interaction results, with higher decoding accuracies in young relative to older adults (light blue) and higher decoding accuracies in older relative to young adults (violet). Statistical maps (TFCE, $p < 0.05$) are superimposed on an individual anatomical image normalized to the MNI space. MNI x coordinates are indicated for each slice.

4. Discussion

The present study aimed at comparing brain activity in young and older adults during fast processing of objects in natural scenes. Accuracy on the categorization task was equivalent between young and older participants for congruent scenes, and both age groups showed

impaired performance when objects were embedded in incongruent contexts. Within-subject drop of performance due to scene incongruence (in terms of accuracy and RT) was more pronounced in older relative to young participants, in agreement with our previous behavioral study (Rémy et al., 2013). Univariate and multivariate analyses reported in the present study controlled for group and condition effects on categorization performance, by including only correct trials and covarying out trial RTs. With this control, fMRI data revealed three main results. First, in scene-selective cortex, there was no evidence for any age differences in levels or patterns of fMRI activity. In both age groups, incongruent scenes induced a higher PHC and OPA BOLD response and less accurate context decoding, when compared to congruent scenes. Second, object-selective cortex was found to decode between congruent and incongruent scenes in young adults, with this decoding being at chance level in older adults. Moreover, a left fusiform region anterior to the LOC responded selectively to scene incongruence in the aged group, with levels of activity inversely related with categorization performance. Third, older individuals' lateral frontal activity was increased when processing incongruent scenes. This age-related increase was not related with task performance, and scene congruence decoding in the same prefrontal regions was less accurate in older participants relative to younger ones.

Our imaging results did not evidence any differences between age groups regarding involvement of scene-selective cortex (i.e. PPA, OPA and RSC) in response to flashed natural scenes. This result is in agreement with preserved fast gist extraction, as suggested by older adults' maintained performance during rapid categorization of briefly-presented natural objects or scenes (Agnew & Pilz, 2017; Lenoble et al., 2013; Ramanoël et al., 2015). Our imaging results are also consistent with preserved neural processing in the PHC during passive exploration of natural scenes (Chee et al., 2006) or during categorization of outdoor/indoor scenes based on LSF coarse features (Ramanoël et al., 2015), as previously observed in older participants. When objects were presented in incongruent contexts, higher activations in the PHC, including the PPA, were found in both age groups. In young adults, this finding is in line with our preceding results on a separate group of participants, using a different set of congruent and incongruent scenes (Rémy et al., 2014). It has been shown that PPA activity may be sensitive to low-level parameters such as spatial frequency content or contrast (Berman & Walther, 2014; Kauffmann, Ramanoël, Guyader, Chauvin, & Peyrin, 2015; Rajimehr, Devaney, Bilenko, Young, & Tootell, 2011), or to scene

category (Henderson, Larson, & Zhu, 2007) or openness (Kravitz, Peng, & Baker, 2011). In the present study, stimuli were highly controlled in terms of visual properties. Quadrettes of scenes were designed with two objects (animal/piece of furniture) embedded in two contexts (natural/indoor), controlling for object size and position, scene contrast and luminance (Fize et al., 2011). Therefore visual features for objects and contexts were similar between congruent and incongruent conditions and only the object/context association varied between conditions. Thus increased activity in the PPA could not be driven by differences in scene visual properties. The PPA, and more globally the PHC, has been proposed to sustain representations for learned relationships between real-world (Bar, Aminoff, & Schacter, 2008; Gronau et al., 2008) or meaningless (Aminoff et al., 2007; Aminoff & Tarr, 2015) objects. Consistently PHC activity has been found to increase when viewing scenes with rich contextual associations relative to scenes evoking less associations (Bar et al., 2008). Our MVPA results showed that context category decoding in the PPA was less accurate when an incongruent object was embedded in the scene. However PPA patterns of activity did not dissociate congruent from incongruent scenes. This indicates that the increase in average BOLD response was not specifically related with deviance or novelty detection, when processing unfamiliar contextual associations. Rather, perception of an object incongruent with its surrounding context may have resulted in supplemental processing in the PHC, due to simultaneous activation of representations that have not been repeatedly co-activated through lifelong experience (Fabre-Thorpe, 2011; Joubert et al., 2008). Objects (animals and pieces of furniture) may have triggered specific contextual associations (Moshe Bar, Aminoff, & Ishai, 2008; Moshe Bar, Aminoff, & Schacter, 2008), different from those triggered by their surrounding context. Accordingly, incongruent scenes elicited less distinctive patterns of activity in the PHC, resulting in lower context decoding accuracy. Conversely, in response to congruent scenes, activation of highly co-occurring object and context representations, i.e. *schemata*, may have induced more specific and reduced PHC activity, possibly through inhibitory connections between object- and scene-selective regions (Mullin & Steeves, 2013). This hypothetical mechanism was supported in our data, showing highly accurate context decoding and lower BOLD response in both age groups. Since visual processing for familiar stimuli was found to stay better preserved with age (Billino & Pilz, 2019), *schemata* may be likewise strengthened in older adults.

In object-selective cortex, accuracy of scene congruence decoding was above chance in the fusiform gyrus (vicinity of collateral sulcus), suggesting specific neural activity in response to object-context unfamiliar relationships. Moreover in young participants, above-chance classification between congruent and incongruent scenes was found in the LOC functional region, although no differences were observed in levels of BOLD response between both conditions. Contextual effects in young adults have been previously reported in object-selective regions (Jenkins et al., 2010; Kim & Biederman, 2011; Kirk, 2008). Interestingly, activity in the LOC has been found to differentiate between semantically-related and unrelated objects (Gronau et al., 2008; Kim & Biederman, 2011) and between real-life scenes depicting human actions with congruent and incongruent objects (Faivre, Dubois, Schwartz, & Mudrik, 2019). Specific patterns in response to incongruent object-context associations, and independently of object or context categories, may reflect detection of mismatch between current perception and existing representations. Such type of associative mismatch signal has been evidenced in the hippocampus, in response to changes in spatial object-context relationships within encoded natural scenes (Howard et al., 2011). Moreover, the fusiform gyrus has been implied in deviance detection during a semantic oddball task (Strange, Henson, Friston, & Dolan, 2000). Likewise, detection of mismatch between predicted and actually perceived (unfamiliar) object-context associations may occur in the fusiform gyrus. The latter result is in line with involvement of the fusiform gyrus in associative processing of object-context relationships (Goh et al., 2004). Context- and object-processing pathways are known to interact at an early stage, notably through reciprocal connections between LOC and PPA (Mullin & Steeves, 2011, 2013). It has been inferred that scene-selective regions may modulate processing of degraded objects in the LOC through feedback mechanisms (Brandman & Peelen, 2017), subtending contextual facilitation of object recognition. However previous behavioral studies using flashed natural scenes have shown that incongruent object-context associations impair fast object or context categorization for RTs as short as 260 ms (Joubert et al., 2008; Joubert, Rousselet, Fize, & Fabre-Thorpe, 2007), suggesting interaction between parallel feedforward streams processing object and context (Fabre-Thorpe, 2011). As visual scenes were unmasked in our experiment, the present fMRI data cannot elucidate which processing mechanisms (feedforward and/or feedback) contributed to the

observed mismatch response in the fusiform area, and further investigation using techniques with higher temporal resolution is clearly needed.

In older adults, decoding between congruent and incongruent scenes was at chance level in the LOC, and scene congruence decoding was significantly more accurate in young vs. older participants in the lateral middle occipital cortex. This may indicate age-related reduction of contextual effects in object-selective cortex. Moreover a fusiform region anterior to the LOC evidenced increased activity in response to incongruent scenes only in the older group, with this activity inversely related to task performance. More accurate scene congruence decoding in older relative to young participants was also observed in the anterior fusiform gyrus. As this region was distinct from object- and context-selective regions evidenced in our data, our set of results may indicate a neural response to non-preferred stimuli in older adults. This response was enhanced when task difficulty increased (i.e. for incongruent scenes) and in aged participants with lower performance on the task. Broadening of neural activity in high-level ventral cortex has been reported in older adults. In particular, increased fusiform activation was found in response to scenes (D. C. Park et al., 2004; J. Park et al., 2012) and has been linked to reduced neuronal selectivity with age (Burianová et al., 2013). Our present data are in line with these previous results, and may reflect unspecific ventral activity that could relate with visual task difficulty and performance. However, our experimental design did not allow direct assessment of the ventral dedifferentiation hypothesis, and further investigation is needed to determine its impact on fast processing of environmental scenes.

A last important result in our study was the increase of middle frontal activity in response to incongruent relative to congruent scenes, which was observed only in older participants.

Additional prefrontal recruitment may reflect the use of top-down attentional resources to perform the task (Biehl et al., 2017; Ramanoël et al., 2015), whereas focused attention was likely less required in young adults (Fabre-Thorpe, 2011; Poncet, Reddy, & Fabre-Thorpe, 2012).

Several studies on a variety of tasks have reported increased prefrontal recruitment with age, in accordance with the PASA model (Davis et al., 2008). Additional prefrontal activity in older adults may reflect functional compensation for reduced ventral activity during successful scene encoding in short- or long-term memory (Gutchess et al., 2005; Park et al., 2003). Age-related prefrontal recruitment has been also consistently reported in several perceptual tasks (Burianová et al.,

2013; Goh et al., 2010; Grady et al., 1994; Levine et al., 2000). In our study, accurate scene congruence decoding was observed in the middle frontal cortex, suggesting that frontal activity in response to scenes reflected specific detection and/or processing of contextual violations (Faivre et al., 2019; Mudrik et al., 2010; Strange et al., 2000). Scene congruence decoding accuracy in the frontal cortex was reduced in older relative to young participants, indicating that mismatch processing may have been less efficient in older adults. Previous studies have proposed a compensatory role for the prefrontal cortex in difficult visual discrimination tasks. During face processing, fronto-temporal connectivity was shown to correlate with performance on a facial identity-matching task (Burianová et al., 2013), and increased prefrontal activity may permit older adults to perform at the level of young adults for low or moderate task demands (Goh et al., 2010). In the latter studies, prefrontal activity was possibly reflecting top-down effects related to stimulus visual exploration and selective attention. Older adults' ocular explorativeness of scenes has been found to positively correlate with subsequent scene-patch recognition accuracy (Açik et al., 2010), indicating efficient exploration processes in visual discrimination tasks. Such explorative strategies could not be used in our fast categorization task, which may explain the discrepancy between our results and those reported during visual discrimination (Burianová et al., 2013; J. O. Goh et al., 2010). Our data rather suggest that older adults' frontal activity represented attentional effects, which were not efficient and did not contribute to improve task performance. This interpretation is in line with an age-related nonspecific prefrontal response during short- and long-term memory tasks (Morcom & Henson, 2018), showing a global increase in average BOLD response but less information carried in multivariate patterns of this BOLD response. In summary, our data show that with just a brief glance at a natural scene, older adults are impaired in categorization of objects presented in incongruent contexts. Fast context processing in scene-selective regions of the ventral pathway seemed well preserved with age. Incongruent object-context associations elicited increased PHC activity in both young and older adults, possibly reflecting activation of multiple representations associated with both object and context. Contextual effects were observed in object-selective regions, likely indicating mismatch detection in response to incongruent scenes. These contextual effects were reduced in older participants. Finally in the aged group, we found an increase in fusiform and prefrontal average BOLD responses to incongruent scenes. These responses were most likely unspecific, and did not

contribute to improve task performance. In daily ecological conditions, sudden changes in surrounding context can occur, for example when opening a door and perceiving a new scene, or when making large head movements. Impairment in rapid scene perception, as demonstrated in our study, may affect older adults' ability to respond to unexpected environmental stimuli, and possibly impact activities in daily life (Hampstead, Stringer, Stilla, Amaraneni, & Sathian, 2011; Rodríguez-bailón, García-morán, Montoro-membila, & Ródenas-garcía, 2017).

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Legends to figures

Supplementary Fig. 1. Within-group effects comparing Congruent and Incongruent conditions (upper part: young group, lower part: older group). The left part shows group results of the univariate analysis, with regions evidencing a higher BOLD response to incongruent vs. congruent scenes. The right part shows decoding accuracy results: regions decoding object and context in congruent scenes in red, regions decoding scene congruence in blue, regions decoding object and context with a higher accuracy in congruent vs. incongruent scenes in yellow. Statistical maps (TFCE, $p < 0.05$) are superimposed on an individual anatomical image normalized to the MNI space. MNI x coordinates are indicated for each slice.

Table 1

Demographic, neuropsychological and visual ability data for groups of participants

	young (<i>n</i> = 21)	older (<i>n</i> = 24)	<i>p</i>
Age (years)	24.3 ± 2.9	66.1 ± 5.1	
Gender	11M, 10F	9M, 15F	0.32
Education (years)	13.8 ± 2.9	14.1 ± 3.3	0.73
Neuropsychological data			
MMSE	29.4 ± 0.8	29.0 ± 1.1	0.15
FCSRT			
immediate recall (/16)	15.8 ± 0.4	15.7 ± 0.6	0.48
sum of free recalls (/48)	38.95 ± 4.6	33.46 ± 5.5	0.0007
sum of free + cued recalls (/48)	47.57 ± 0.8	47.00 ± 1.4	0.10
delayed free recall (/16)	15.09 ± 0.9	13.08 ± 2.1	0.0002
delayed free + cued recall (/16)	15.91 ± 0.3	15.92 ± 0.3	0.89
recognition (/16)	15.95 ± 0.2	15.65 ± 0.9	0.13
phonemic verbal fluency	28.7 ± 6.3	29.1 ± 7.9	0.85
semantic verbal fluency	38.9 ± 8.2	34.5 ± 10.7	0.13
DO80	78.84 ± 3.0	79.74 ± 0.5	0.21
PPTT	53.50 ± 1.3	53.48 ± 1.4	0.96
WAIS-III digit span: forward	7.24 ± 1.7	6.54 ± 1.6	0.16
WAIS-III digit span: backward	6.14 ± 1.9	5.62 ± 1.5	0.32
digit-symbol test (/90)	65.14 ± 10.7	49.37 ± 10.6	0.00002
Visual abilities			
Armaignac (13.6 / 10.6 / 8.2)	19 / 2 / 0	15 / 4 / 5	0.06
Pelli-Robson (1.95 / 1.65 / 1.35)	17 / 4 / 0	19 / 5 / 0	0.88

Data are mean ± standard deviation.

FCSRT, free and cued selective recall reminding test; PPTT, Pyramids and Palm Trees Test.

Table 2Univariate GLM effects of scene incongruence ($n = 45$, TFCE-corrected $p < 0.05$)

Brain region		local peaks				cluster extent ¹
		<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i> -value	
<i>Incongruent > Congruent scenes</i>						
Parahippocampal gyrus	L	-36	-24	-24	5.37	88
Fusiform gyrus	L	-30	-39	-21	5.02	
Parahippocampal gyrus	R	35	-27	-21	5.08	85
Fusiform gyrus	R	36	-39	-18	5.66	
Orbitofrontal cortex	L	-39	33	0	4.96	32
Hippocampus	R	27	-6	-18	4.56	28

¹ in $2 \times 2 \times 2$ mm³ voxels

Table 3Univariate GLM congruence effects on brain activity within each age group (TFCE-corrected $p < 0.05$)

Brain region		local peaks			t-value	cluster extent ¹
		x	y	z		
Young group						
<i>Congruent scenes > Incongruent scenes</i>						
Insular cortex	R	36	3	-6	4.69	156
Superior temporal gyrus	R	51	-12	-3	4.06	
Inferior parietal lobe	R	27	-39	57	3.98	222
Precuneus		3	-33	57	3.59	
<i>Incongruent scenes > Congruent scenes</i>						
Hippocampus	R	24	-9	-18	4.31	72
Older group						
<i>Incongruent scenes > Congruent scenes</i>						
Middle frontal gyrus	R	42	30	24	5.30	253
Inferior frontal gyrus	R	39	3	27	4.79	
Fusiform gyrus	L	-45	-51	-18	5.28	415
Parahippocampal gyrus	L	-33	-39	-21	4.60	
Parahippocampal gyrus	R	36	-39	-21	5.01	306
Fusiform gyrus	R	51	-45	-18	4.30	
Inferior frontal gyrus	L	-36	33	-3	4.74	130
Middle frontal gyrus	L	-45	24	30	4.71	282
Inferior frontal gyrus	L	-39	9	30	4.41	
Superior occipital gyrus	R	33	-66	36	4.01	198
Inferior parietal lobe	R	36	-60	45	3.77	

¹ in $2 \times 2 \times 2$ mm³ voxels

Table 4Univariate GLM Age × Congruence interaction (TFCE-corrected $p < 0.05$)

Brain region		local peaks				cluster extent ¹
		x	y	z	t-value	
<i>Congruence effect: Incongruent scenes > Congruent scenes</i>						
<i>Older > Young</i>						
Middle frontal gyrus	R	42	30	24	5.03	88
Fusiform gyrus	L	-45	-48	-18	4.69	63
Middle frontal gyrus	L	-42	24	30	4.44	49
Fusiform gyrus	R	-42	-50	-18	4.30	50
<i>Young > Older</i>						
Pons	R	6	-30	-24	4.39	48

¹ in $2 \times 2 \times 2 \text{ mm}^3$ voxels

Figure S1

