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False recognitions in short-term memory – Age-differences in neural activity

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Abstract
While the knowledge on age-related differences in susceptibility to episodic false memories is extensive, little is known about this phenomenon in visual short-term memory (STM). Our previous behavioural research indicated that older adults are more confident of their erroneous STM recognitions than young adults. However, unlike in episodic memory, we did not find support for older adults' higher rate of false alarms. To further understand this specific age-difference, here we investigated its neural correlates. First, the pattern of behavioural results replicated the one from our previous experiment. Second, younger adults, when compared to older adults, exhibited higher false recognition-related activity of the visual cortex, the anterior cingulate cortex, the frontal operculum/insular cortex as well as regions within the anterior and dorsolateral prefrontal cortex. No age-differences were observed in hippocampal activity. Third, younger but not older adults presented higher activity in the anterior cingulate cortex and the frontal operculum/insular cortex for false recognitions when compared to highly confident correct rejections. Finally, frontal activity was influenced by both the individuals' performance and their metacognitive abilities. The results suggest that age-related differences in confidence of STM false recognitions may arise from age-differences in performance monitoring and uncertainty processing rather than in hippocampal-mediated binding.

Keywords:
Visual short-term memory
Age-related differences
False recognitions
Confidence judgements
Monitoring
Neural correlates

1. Introduction

False recognitions and recall of material that has never been presented are widely studied in the context of episodic memory, both with regard to their neural mechanisms (for review see Kurkela & Dennis, 2016) as well as age-related differences (for review see Devitt & Schacter, 2016). Older adults are generally more susceptible to false memories (Devitt & Schacter, 2016) and more confident of erroneous recognitions (Dodson, Bawa, & Krueger, 2007; Dodson et al., 2015; Shing et al., 2009). When individuals consider false memories as genuine with high confidence, this is commonly interpreted as *misrecollection*, i.e. illusory but detailed recollections of miscombined material resulting from binding impairments (Dodson, Bawa, & Slotnick, 2007), or as a joint effect of deficits in binding and performance monitoring (Fandakova et al., 2013b).

False memories are also observed in the short-term memory (STM; Abadie & Camos, 2019; Atkins & Reuter-Lorenz, 2008; Coane, McBride, Raulerson, & Jordan, 2007; Lewandowska, Gągol, Sikora-Wachowicz, Marek, & Fąfrowicz, 2019; Lewandowska, Wachowicz, Marek, Oginska, & Fafrowicz, 2018). Two frameworks were proposed to explain their occurrence and characteristics within this context: a unitary view suggesting common or partially common/partially unique mechanisms underlying false alarms at short- and long-term (Atkins & Reuter-Lorenz, 2008, 2011; Flegal, Atkins, & Reuter-Lorenz, 2010; Flegal & Reuter-Lorenz, 2014), and a complementary view suggesting that short-term false alarms result from long-term memory gist (see Abadie & Camos, 2019). The latter, however, is unlikely to explain false recognitions for stimuli with no pre-existing semantic representations, especially when the active maintenance is not distorted by the distractor (see also Sikora-Wachowicz et al., 2019).

While age-related differences in STM functioning are widely studied, including studies concerning the impact of binding abilities (Peterson & Naveh-Benjamin, 2016; Rhodes et al., 2017) and top-down control (Gazzaley et al., 2005), little is known about age-related differences in the susceptibility to and characteristics of false memories. It is noteworthy that, similar to episodic memory, age-related differences in STM were proposed to reflect changes in both binding and top-down control (Sander et al., 2012; Sander et al., 2011). Accordingly, older adults may be more susceptible to false recognitions and more confident of their errors also in STM. However, in a previous study, we found support only for older adults' higher confidence following false recognitions, but not for a higher rate of false memories (Sikora-Wachowicz et al., 2019). These results may suggest that in visual STM, age-differences in confidence accompanying false recognitions result from differences in memory monitoring (see Sikora-Wachowicz et al., 2019).

At the neural level, older adults' higher susceptibility to high-confidence false recognitions in episodic memory was linked with senescent changes in the medial temporal lobe (particularly hippocampus) and prefrontal cortex (Fandakova et al., 2014; Fandakova et al., 2013a; Fandakova et al., 2013b). In addition, age-related differences in false memories were also linked with changes in the activity of the cingulo-opercular regions (Fandakova, Sander, et al., 2018). Importantly, to date, there are no studies targeting age-related differences in neural activity linked with false recognitions in visual STM. The two extant studies looking at neural correlates of false STM did not address the age- differences (Atkins & Reuter-Lorenz, 2011; Iidaka et al., 2014). However, there is a number of studies suggesting that the neural mechanisms underlying long-term memory and STM are at least partially overlapping (e.g. Ranganath & Blumenfeld, 2005), including the role of the hippocampus in binding (e.g. Libby et al., 2014).

In the context of episodic memory, based on animal studies Wilson et al. (2006) suggested that misrecollections result from age-related strengthening of the auto-associative network activity in the hippocampus' CA3 region and diminished dentate gyrus activity, resulting in enhanced binding and reduced ability to separate overlapping patterns, respectively. In addition, numerous reports provide evidence for CA3 involvement also in pattern separation (for a review see Yassa & Stark, 2011). In line with this, a study by Shing et al. (2011) indicated that older adults' higher rate of false alarms is linked with reduced volume of the dentate gyrus–CA3/4 region of the hippocampus. The hippocampus was also found to be involved in some STM tasks, especially when processing of relations (Hannula et al., 2006), pairs (Olson et al., 2006) or complex high-resolution stimuli (Yonelinas, 2013) was required. However, its role in STM is much more ambiguous than its well- established role in long term memory (e.g. Olson et al., 2006; Yonelinas, 2013).

Both the activity of the prefrontal cortex and its functional connectivity with the medial temporal lobes were also linked with age-related differences in the effective processing of familiar information and susceptibility to episodic false memories (Fandakova et al., 2014; Fandakova et al., 2015). For instance, the activity of the anterior prefrontal cortex (APFC) was linked both with age-differences in performance in the presence of increasing task' monitoring demands (Fandakova et al., 2014), and with metamemory and cognitive control abilities (Fandakova, Bunge, et al., 2018). Also, the activity of the dorsolateral prefrontal cortex (DLPFC), a region associated with top-down executive control (Gazzaley & Nobre, 2012), can be linked with an adequate assessment of false alarm-related confidence. The level of confidence after errors was negatively correlated with performance on the Wisconsin Card Sorting Test (WCST, Fandakova et al., 2013b), serving as a measure of frontal lobe functioning and linked with the DLPFC activity (e.g. Berman et al., 1995). In addition, the decreased DLPFC activity was associated with false recognitions in STM (Atkins & Reuter-Lorenz, 2011), suggesting that also at short lags there is a link between false alarms and diminished cognitive control. Furthermore, age-related differences in metamemory, uncertainty processing and performance monitoring abilities were also linked with changes in the dorsal anterior cingulate cortex (dACC), frontal operculum cortex / anterior insula (FO/ AI) and ventromedial prefrontal cortex (VMPFC; Fandakova, Sander, et al., 2018; Fandakova et al., 2017). For instance, older adults, unlike younger adults, did not present the modulation of the dACC-AI activity regarding the fidelity of memory representations (Fandakova, Sander, et al., 2018). It suggests that they did not selectively engage processes linked with error monitoring and uncertainty.

The aim of the current study was to investigate the neural mechanisms underlying short-term false recognition in younger and older adults. We planned to test the age-related differences in these mechanisms, and to assess the impact of individuals' ability to adjust the confidence level according to response accuracy. Considering the evidence on the effects of frontally-mediated monitoring (e.g. Fandakova et al., 2013b; Fandakova, Sander, et al., 2018) and the important role of top-down control in efficient STM functioning (Gazzaley et al., 2005; Gazzaley & Nobre, 2012), we expected that older adults' deficits therein may be crucial for the differences in high-confidence short-term false recognitions. Specifically, we assumed that during false recognitions younger but not necessarily older adults will demonstrate an increase in activity of brain regions linked with error monitoring and uncertainty processing (see Fandakova, Sander, et al., 2018). We also assumed that in a direct comparison, younger adults, compared to older adults, will present higher false alarm-related activity in frontal regions linked with performance monitoring and cognitive control, and that these age- differences will be related to older adults' less adequate assessment of confidence after errors. In addition, given the results from our behavioural experiment (Sikora-Wachowicz, et al., 2019) and the ambiguous findings regarding the role of hippocampus in STM tasks (Hannula et al., 2006; Olson et al., 2006), we explored whether changes in the hippocampus activity will be observed related to false memories and whether there will be age-differences therein. In addition, we aimed to replicate the behavioural results obtained in our previous experiment.

2. Materials and Methods

2.1 Participants

Fifty-one volunteers: twenty-five young (YA; $\mathrm{M}_{\mathrm{age}}$ 24.2 y, SD = 3.1, 13 females) and twenty-six older adults (OA; $\mathrm{M}_{\mathrm{age}}$ 65.5 y, SD = 4.6, 15 females) without major psychiatric and neurological disorders and contraindications for MRI scanning participated in the study. One younger adult was excluded due to a lack of FAs and three older adults were excluded due to technical problems during data collection or problems with following the task routine. Thus, the final sample for all analyses consisted of twenty-four YA ($\mathrm{M}_{\mathrm{age}}$ 24.2 y, SD = 3.1, 13 females) and twenty-three OA ($\mathrm{M}_{\mathrm{age}}$ 65.0 y, SD = 4.7, 14 females). All participants in the final group were right-handed as indicated by the Edinburgh Handedness Inventory (Oldfield, 1971), and had a normal or corrected-to-normal vision. Participants from both age groups did not differ in terms of years of education: YA M 16.29 $\pm$ 3.54; OA M 16.5 $\pm$ 2.95; $t_{(45)}$ = -0.22, p = 0.83, nor in terms of depression symptoms as measured by the Beck Depression Inventory (BDI; Beck and Steer, 1993): YA M 6.43, SE = 0.89, OA M 5.59, SE = 1.55; $t_{(45)} = 0.47$, p = 0.64. Older participants presented no symptoms of dementia, as indicated by the Mini-Mental State Examination Scale (MMSE; Folstein et al., 1975): M 29.48, SD = 0.73. Younger adults were students recruited at the Jagiellonian University, Krakow, Poland, whereas older adults were recruited from the local community. All participants were familiarized with the procedure and gave written informed consent before participating. The experiment was approved by the Committee for Research Ethics at the Institute of Applied Psychology at the Jagiellonian University and conducted in accordance with the Declaration of Helsinki.

2.2 Experimental procedure and stimuli

In order to study age-related differences in false memories in visual STM, we used a modified version of an item-based recognition task with single abstract objects as targets and subsequent confidence judgements (see Sikora-Wachowicz et al., 2019), adjusted to the requirements of the fMRI study. The task was based on paradigms used to study false memories (e.g., Garoff-Eaton et al., 2006; Dennis et al., 2014, Dennis et al., 2014; see also Kurkela & Dennis, 2016) and specifically adjusted to STM (e.g., Lewandowska et al., 2019; Lewandowska et al., 2018; Sikora-Wachowicz et al., 2019). Unlike in the change detection tasks, commonly used to study VSTM capacity (e.g., Todd & Marois, 2004; 2005; Sander et al., 2011), in this type of false memory tasks the performance is critically dependent on the perceptual or conceptual similarity between stimuli in a memory set and a lure presented at recognition. Whereas in a classic DRM paradigm lists of semantically-related words are memorized (Deese, 1959; Roediger & McDermott, 1995), different set sizes and material types have been used ever since (e.g., Ly, Murray, & Yassa, 2013; Pidgeon & Morcom, 2014). In the present study, in order to limit the possible influences from the long-term memory gist, single abstract objects were used as targets and a visual mask was introduced instead of a distractor (Abadie & Camos, 2019 see also Sikora-Wachowicz et al., 2019). As prefrontally-mediated monitoring and executive control are crucial for working memory functioning (Gazzaley & Nobre, 2012), we assumed that these processes are primarily involved in mediating false alarms within the task. Yet, as the stimuli used within the study are rather complex, we also assumed the possible impact of high-resolution hippocampally-mediated binding (see Yonelinas, 2013).

Participants were presented with 120 trials: 50 of which included a positive memory probe (target), 50 a probe similar to the target (lure), and 20 a negative, clearly distinct probe (foil). In each trial, participants were first presented with a single abstract object as a target (1000ms), followed by a fixed 800ms inter-stimulus interval (ISI). Then, after a visual mask (2200ms) and a second ISI (skewed jittering, 1000-9000ms, avg. 3316.67ms), the memory probe appeared for 2000ms, and participants had to decide whether the presented item is the same as or different from the target. Finally, after an additional fixed ISI (1000ms), the individuals were asked to assess the confidence of their recognition response (2000ms) on a 3-point scale (from 1 – unsure to 3 – sure). Confidence judgements were then followed by an inter-trial interval (skewed jittering, ITI; 3000-15000ms, avg. 6000ms) with a fixation point displayed on the screen (see Fig. 1).

To ensure that each stimulus is followed by each probe type (including a foil), we created six versions of the procedure and counterbalanced these across participants. In order to minimize the effect of head movements during the data acquisition, the procedure was divided into two predetermined, equally difficult runs (60 trials each) and the order of runs was also counterbalanced. The sequence was optimized using Optseq2 toolbox (surfer.nmr.mgh.harvard.edu/optseq) to enable separating the hemodynamic response from the stage of encoding and retrieval for different probe types. Within each version, the order of stimuli was randomized. The order of probe types within a run, and the jittering of ISIs and ITIs were fixed in a manner established by Optseq2, but counterbalanced - half of participants started with version from one run, and half with version from the other. It resulted in altogether twelve versions of the procedure. The ISI between recognition and confidence judgement was not jittered, following the rationale that the processes of postretrieval monitoring cannot be separated in time from the recognition process. In addition, to avoid participants' habituation for a visual mask, ten very similar grey masks were implemented and randomized within the procedure. The selected response time window was longer than the older adults' responses time previously reported in the short-term memory tasks (e.g. Oberauer, 2005), and our pilot results also indicated that it is sufficient for older adults to respond.

The experimental task was presented with E-Prime 2.0 (Psychology Software Tools) on a 32-inch screen located about 120 cm behind the participants' head. All stimuli were shown at the centre of the screen. The abstract objects occupied 6° 13' of visual angle, and the visual mask 13° 56' × 8° 35' of visual angle. Stimuli were presented in dark grey (RGB 72, 72, 72) on a light grey (RGB 176, 176, 176) background and they were previously used in similar STM tasks (Lewandowska et al., 2019; Lewandowska et al., 2018; Sikora-Wachowicz et al., 2019). Participants provided responses with Celeritas Fiber Optic Response System (©Psychology Software Tools). During the recognition test, they pressed buttons under the index and middle finger of their right hand, for 'same' and 'different' response respectively. To make a confidence judgement, participants used they left hand: index, middle or ring finger were used for 'sure', 'semi-sure', and 'unsure' responses respectively.

2.3 Image acquisition

Magnetic resonance imaging (MRI) data was collected on a 3T scanner (Magnetom Skyra, Siemens) with a 64-channel head/neck coil. Head movements during scanning were minimized with the use of foam pads placed around the participant's head. High-resolution anatomical images were acquired prior to the fieldmap and functional data, with use of a T1-weighted MPRAGE sequence: $\mathrm{TR} = 1800\text{ms}$, $\mathrm{TE} = 2.37\text{ms}$, $\mathrm{FOV} = 250\text{mm}$, $\text{voxel size} = 0.9\ \text{mm}^3$, GRAPPA acceleration factor 3, and prescan normalize on. Functional T2* blood oxygenation level- dependent (BOLD) whole-brain images were acquired using an EPI sequence: 45 slices were taken in an interleaved, ascending manner, TR

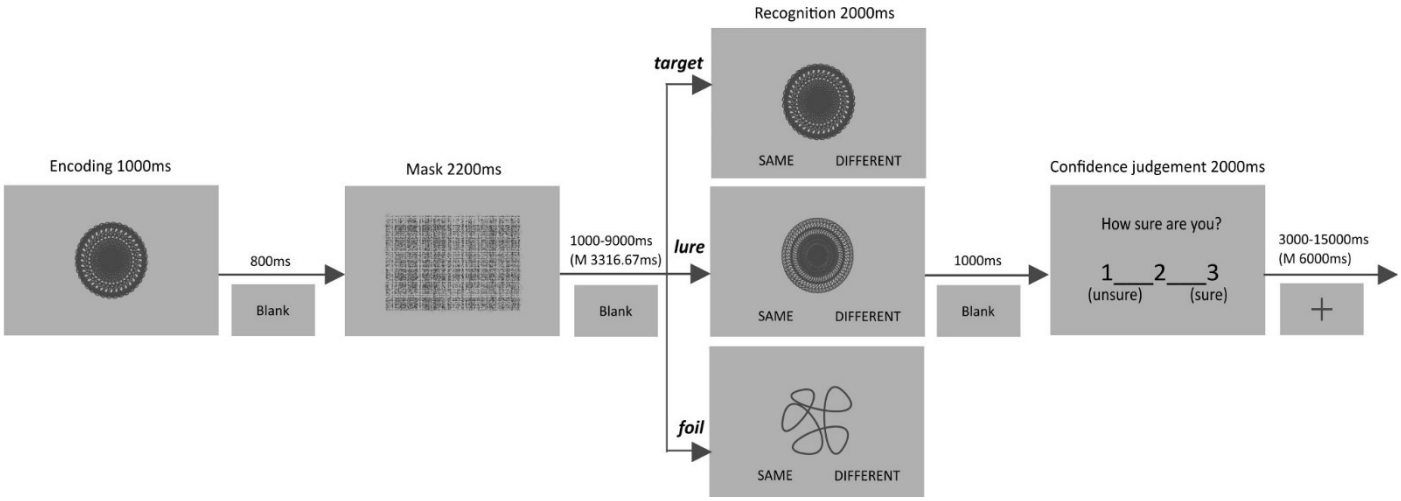

Fig. 1. Illustration of the design and procedure of the experimental task

$= 2200$ms, $\mathrm{TE} = 27$ms, $\mathrm{flip\ angle} = 75$ deg., $\mathrm{FOV} = 216 \times 216 \times 135$ mm, $\mathrm{voxel\ size} = 3$ mm^3, phase encoding A/P, GRAPPA acceleration factor 3, shim mode advanced, and prescan normalize on. There were two EPI runs, each consisting of 504 measurements and lasting 18 minutes and 41 seconds, with a short break between them. The first four volumes (dummy scans) of each run were discarded by the scanner to provide a steady tissue magnetization. Fieldmap images ($\mathrm{TR} = 508$ms, $\mathrm{TE}\ 1 = 4.92$ms, $\mathrm{TE}\ 2 = 7.38$), allowing for reconstruction of magnitude and phase image of a magnetic field, were collected before functional scans with identical voxel size, slice number, and position parameters.

2.4. Behavioural data analyses

All statistical analyses were conducted using Statistica 13.3 software (StatSoft, Inc.), except the Bayesian analyses made using JASP 0.10 software (JASP Team). Data was pre-processed with Matlab 2015a (Mathworks, Inc.). A detailed description of each statistical test is provided in the Results section.

2.5. Functional data analyses

Functional magnetic resonance imaging (fMRI) data underwent standard pre-processing with FSL (FMRI Expert Analysis Tool, FMRIB's Software Library, version 6.00, www.fmrib.ox.ac.uk/fsl; Jenkinson et al., 2012). T1-weighted anatomical images were skull-stripped using Brain Extraction Tool in FSL (BET; Smith, 2002). The fieldmap magnitude images were skull-stripped and eroded by one voxel along each axis, to obtain the tight mask excluding all non-brain voxel, and the calibrated fieldmap in rad/s was prepared with *fsl_prepare_fieldmap*. The fMRI data was despiked with a *3dDespike* function implemented in AFNI (Cox, 1996), prior to other preprocessing steps. Motion outliers were detected with *fsl_motion_outliers* function used on the raw data and added in the further steps of analyses to censor timepoints with excessive movements (M 3.03% $\pm$ 2.36%; YA: 2.34% $\pm$ 2.10%; OA 3.75% $\pm$ 2.43%). Further steps of preprocessing were carried out using FSL FEAT. All fMRI data was motion-corrected using FSL MCFLIRT (Jenkinson et al., 2002), slice-timing corrected, unwarped (i.e. corrected for B0 distortions; Jenkinson, 2003), skull-stripped using automated BET (Smith, 2002), spatially smoothed using a Gaussian kernel of FWHM 6mm, and high-pass filtered with a 100s cut-off. fMRI data was registered to high-resolution anatomical scans using full search with the BBR algorithm, and, after the first-level statistical analyses, to MNI 152 standard space using full search with 12 DOF as implemented in FSL FLIRT (Jenkinson et al., 2002; Jenkinson & Smith, 2001).

General Linear Model (GLM) analysis was also conducted using FSL FEAT. At the first level, time-series statistical analyses were carried out for each run separately using FILM with local autocorrelation correction (Woolrich et al., 2001). The occurrence of each specific probe type was modelled by convolving a box-car representation of the stimulus with the canonical double-gamma hemodynamic response function (HRF). Ten task-related regressors were established: two for encoding with subsequent correct and erroneous responses, seven related to the stage of recognition: for highly confident hits (HighHit), low- and semi- confident hits, omissions, highly confident correct rejections of lures (HighCR), low- and semi-confident correct rejections of lures, false recognitions of lures (FA), correct rejections of foils, and the regressor 'other' with few encoding and retrieval timepoints for missing responses or errors on foils. As the ISI between target and mask, and the ISI between recognition and confidence judgement were fixed, encoding duration was established for 4 seconds (i.e. together with mask), and retrieval duration for 5 seconds (i.e. together with confidence judgements). In addition, there were six movement parameters and additional regressors for timepoints with motion outliers. On the second level statistical analysis, the lower-level maps for separate runs were used to model single-subject maps (runs average). Fixed-effect higher-level modelling was used (Beckmann et al., 2003; Woolrich, 2008; Woolrich et al., 2004). On the third level statistical analysis, multisubject' data was modelled with mixed-effect assumption using stage 1 of FSL FLAME (Beckmann et al., 2003; Woolrich, 2008; Woolrich et al., 2004).

The contrast of interest was false recognitions (FA) versus high confidence correct rejections of lures (HighCR). Highly confident correct rejection of lure probes most likely involved a 'recall-to-reject' strategy, i.e., unlike in hits and correct rejections of foils, detailed recollection of targets is needed to reject the perceptually-related probe. Moreover, unlike hits, correct rejection of a lure allows for holding constant the novelty of an item. Interference between a perceptually related lure and a previously presented target evokes the need for increased cognitive control: using a CR-based contrast enables us to study differences in top-down processes specifically linked with FAs, while controlling for processing of lures in general. In a similar vein, prior investigations of cognitive processes underlying false memory recognition have argued for the use of FA vs. CR contrasts (Kurkela and Dennis, 2016), also in age comparative studies (e.g., Fandakova et al., 2014; Fandakova, Sander, et al., 2018). A detailed description of each statistical test conducted on the third level is provided in the Results section. Unless specified otherwise, all Z-scored images were thresholded using $\mathrm{Z} > 2.3$ and a corrected cluster significance $p < 0.05$ (Worsley, 2001).

3. Results

3.1. Behavioural results

At the behavioural level, the study was aimed to test whether there are age-related differences in the STM performance.

3.1.1. Accuracy

First, in order to assess the age-related differences in overall performance, the analyses of a sensitivity index (d', see Macmillan & Creelman, 2004) was performed. The d' values were calculated as $d' = z\,(Hit) - z(FA)$, separately from lures and foils, what allowed for an additional assessment whether the procedure was effective in eliciting perceptually-based false memories. Both Hit- and FA-rates were transformed by adding 0.5 to raw scores and dividing by $\mathrm{N} + 1$, where N is the number of targets and lures or foils, respectively (see Snodgrass & Corwin, 1988). A mixed measures ANOVA with probe type as a within-person factor (d' derived from targets and lures vs. d' derived from targets and foils) and age as a between-person factor (YA vs. OA) revealed a significant effect of probe type ($F_{(1,45)} = 286.79$, $p < 0.001$, $\eta_p^2 = 0.86$), indicating that both age groups experienced more problems when discriminating targets from lures than from foils (see Fig. 2). Neither an effect of age nor the interaction effect of age and probe type was observed ($p = 0.36$ and $p = 0.35$, respectively).

In order to specifically address age-related differences in responses

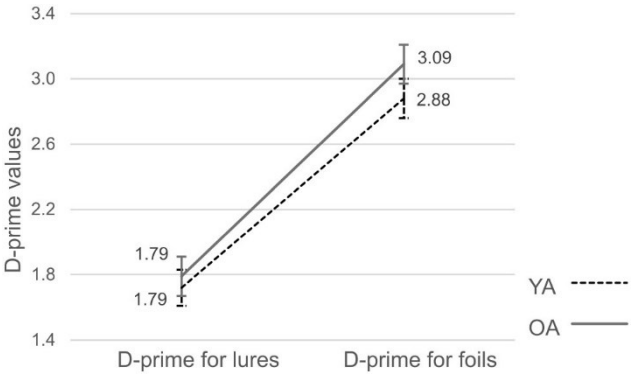

Fig. 2. Mean d' values derived from targets and lures and from targets and foils, for both younger (YA) and older adults (OA). Standard errors are indicated in the brackets.

on each probe type, the proportion of 'same' responses was calculated for each probe type and submitted to a mixed measures ANOVA with response type as a within-person factor (hits, FA to lures, FA to foils) and age as a between-person factor (YA vs. OA). In consistence with the d' analysis, the analyses revealed only the main effect of response type ($F_{(2,90)} = 754.12$, $p < 0.001$, $\eta_p^2 = 0.94$). The HSD Tukey post-hoc test indicated that there were more hits than FA of lures ($p < 0.001$) and foils ($p < 0.001$), and more FA of lures than of foils ($p < 0.001$, see Table 1). Neither the effect of age nor the interaction effect of age and response type was observed ($p = 0.53$ and $p = 0.68$, respectively).

Finally, we tested for age-related differences in false recognitions of lures with a Bayesian analogue of an unpaired t-test. The analysis indicated that the observed data are 3.27 times more likely under H_0 than under H_1 ($BF_{10} = 0.31$ and $BF_{01} = 3.27$), providing moderate evidence for lack of age-related differences in susceptibility to perceptually- related false memories in STM (Doorn et al., 2019).

3.1.2. Confidence

Next, we aimed to test the hypothesis that older adults present poorer metacognitive abilities than younger adults and that this impairment is related to older adults' higher confidence accompanying false recognitions.

First, the age-related differences in this ability to adjust the subjective level of confidence according to the response accuracy were tested with the metacognitive sensitivity index (*type 2 d'*, see Fleming & Lau, 2014). The *type 2 d'* values were calculated as *type 2 d' = z(type 2 hit) – z(type 2 FA)*, where *type 2 hits* stands for high-confidence correct responses as a proportion of all correct responses, irrespective of probe type, and *type 2 FA* stands for high-confidence incorrect responses as a proportion of all incorrect responses, irrespective of probe type. Similarly like in the case of d', both *type 2 hit-* and *type 2 FA*-rates were transformed by adding 0.5 to raw scores and dividing by $N + 1$, where N is the number of all correct or incorrect probes, respectively (see Snodgrass & Corwin, 1988). An unpaired t-test revealed significant age- related differences in *type 2 d'* values ($t_{(45)} = 2.78$, $p = 0.008$), with older adults presenting poorer metamemory than younger adults (see Fig. 3A).

Table 1
The proportion of 'same' responses (i.e., hits, false alarms to lures, false alarms to foils) and 'different' responses (i.e., misses, correct rejections to lures, correct rejections to foils), for both younger (YA) and older adults (OA). Standard errors are indicated in the brackets.

Proportion of responses	'Same' responses		'Different' responses	
Probe type:	YA	OA	YA	OA
targets	0.82 (0.03)	0.86 (0.03)	0.16 (0.02)	0.13 (0.02)
lures	0.26 (0.03)	0.28 (0.03)	0.73 (0.03)	0.71 (0.03)
foils	0.01 (0.01)	0.01 (0.01)	0.98 (0.01)	0.99 (0.01)

Second, we tested age-related differences specifically in lure confidence ratings, i.e. FA and correct rejections (CR) - probe types being of main interest in the fMRI analyses. The mixed-measures ANOVA for average confidence ratings with response type as the within-subject factor (FA vs. CR) and age as the between-subject factor (YA vs. OA) revealed the significant effects of age ($F_{(1,45)} = 10.75$, $p = 0.002$, $\eta_p^2 = 0.19$), response type ($F_{(1,45)} = 73.76$, $p < 0.001$, $\eta_p^2 = 0.62$), and an interaction effect ($F_{(1,45)} = 12.91$, $p < 0.001$, $\eta_p^2 = 0.22$). HSD Tukey post-hoc test indicated that while both age groups presented lower confidence after false recognitions than correct rejections (YA $p < 0.001$, OA $p < 0.05$), the age-related differences in confidence were observed after FAs ($p < 0.001$) but not after CRs of lures ($p = 0.87$; see Fig. 3B). For full model analysis, being behind the scope of this study, see Section 2 in Supplementary Materials.

3.1.3. Reaction time

In order to further explore the age-related differences in STM FA, and to verify whether the differences in performance could be explained by age-related differences in the speed-accuracy trade-off (see Oberauer, 2005), the analyses of probe RT and confidence RT were performed for lure probes. Similar to the analysis of average confidence ratings, the full model analyses are reported in Section 2 in Supplementary Materials.

The mixed-measures ANOVA on probe RT with response type as a within-subject factor (FA vs. CR) and age as a between-subject factor (YA vs. OA) revealed a main effect of response type ($F_{(1,45)} = 39.41$, $p < 0.001$, $\eta_p^2 = 0.47$) and a significant effect of age ($F_{(1,45)} = 16.78$, $p < 0.001$, $\eta_p^2 = 0.27$), but no interaction effect ($p = 0.93$). Older adults' reactions were slower than younger adults, but both age groups needed more time to falsely recognize lure items than to reject it (see Fig. 4A).

The mixed-measures ANOVA on confidence RT with response type as a within-subject factor (FA vs. CR) and age as a between-subject factor (YA vs. OA) also revealed a main effect of response type ($F_{(1,45)} = 9.26$, $p = 0.004$, $\eta_p^2 = 0.17$), but neither the main effect of age nor the interaction effect of age and response type reached significance ($p = 0.09$ and $p = 0.75$, respectively). Time to make a confidence judgement was longer after false recognitions than correct rejections, but the age-related differences were not significant (see Fig. 4B).

In summary, we replicated the main findings from our previous experiment (Sikora-Wachowicz et al., 2019). Namely, we did not observe age-related differences in susceptibility to short-term false recognitions, however, in line with our hypothesis, older adults, compared to younger adults, presented poorer metamemory abilities: They were more confident of their false recognition responses. In addition, participants from both age groups needed more time to make false recognitions than correct rejections.

3.2. fMRI results

The present study aimed to shed a light on the neural mechanisms underlying false recognition in younger and older adults in an item-based STM task and to test whether there are age-related differences in these mechanisms.

3.2.1. FA –related activity in younger and older adults

First, as there is a very limited number of findings regarding neural mechanisms of short-term false recognitions, and they are conducted only on younger participants (Atkins & Reuter-Lorenz, 2011; Iidaka et al., 2014), we aimed to describe the FA-related brain activity for younger and older adults. We wanted to test the hypothesis that while both age groups present FA-related decreases in activity of brain regions linked with retrieval and processing representations in STM, younger but not necessarily older adults present FA-related increases in activity in regions linked with uncertainty processing and monitoring (Fandakova, Sander, et al., 2018). In order to do so, whole-brain analyses (one- sample t-tests) were computed to obtain maps with FA-related activity for each age group separately.

In younger adults, a whole-brain analysis revealed three clusters with FA-related increases compared to HighCR. The clusters involved: (1) medial superior frontal gyrus (mSFG) extending to dACC, (2) left (L) FO extending to the borders of inferior frontal gyrus (IFG) and AI, and (3) an area on the border of right (R) precentral and postcentral gyrus (see Table 2, Fig. 5A). Four clusters with FA-related decreases in activity were identified: (1) involving mainly R lingual gyrus but also lateral occipital cortex and occipital pole, (2) L postcentral and precentral regions, together with precuneus, (3) R parietal operculum and subcortical areas (caudate, parts of the hippocampus), (4) L subcortical areas (caudate, parts of the hippocampus). However, as the clusters exceeded beyond single or neighbouring anatomical areas (see Table S1.1 and Fig. S1.1A in Supplementary Materials), the primary threshold for creating clusters was increased to $Z > 3.1$, in order to report more precise spatial localization of peaks (Woo et al., 2014). It allowed for

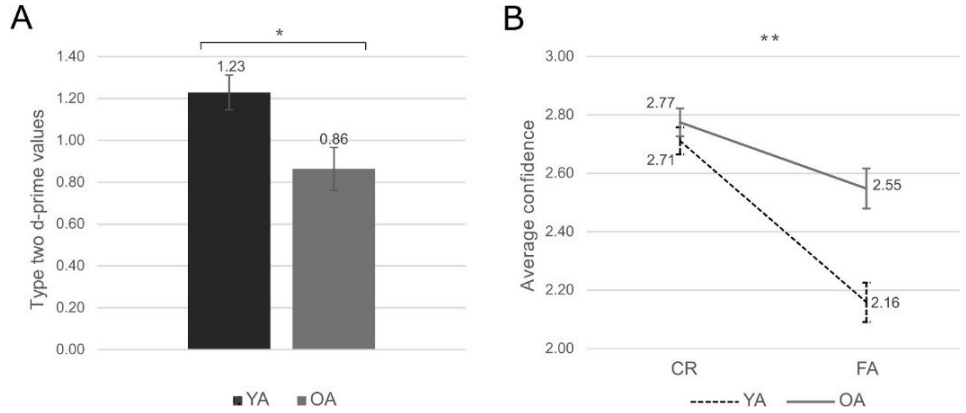

Fig. 3. A. Type two d' values for younger (YA) and older (OA) adults; B. Average confidence ratings. An interaction effect; * p <0.01; ** $p < 0.001$. Error bars indicate standard error. CR – correct rejections, FA - false recognitions of lures.

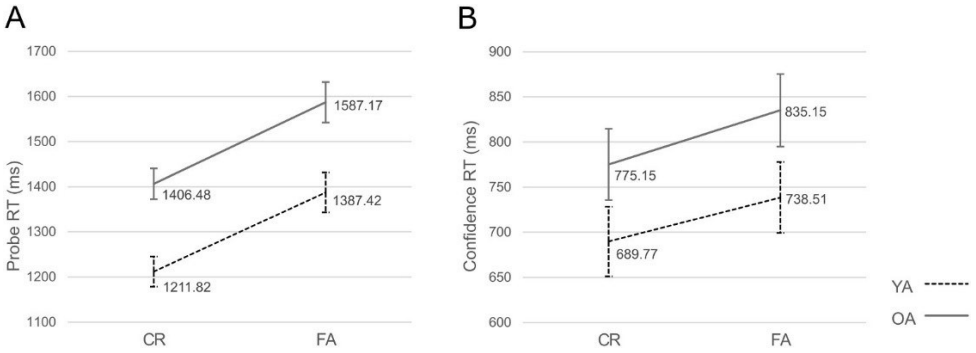

Fig. 4. A. Probe reaction time (RT) for correct rejections of lures (CR) and false recognitions of lures (FA) for both younger (YA) and older (OA) adults. B. Confidence RT for CRs and FAs for YA and OA adults. Standard errors are

Table 2
Peak activations for false recognitions (FA) > highly-confident correct rejection of lures (HighCR) for younger adults (YA), clusters thresholded at $Z > 2.3$, $p_{corrected} < 0.05$; Peak activations for FA < HighCR for YA and for older adults (OA), clusters thresholded at $Z > 3.1$, $p_{corrected} < 0.05$. L – left, R – right, dACC – dorsal anterior cingulate cortex, IFG – inferior frontal gyrus, SFG – superior frontal gyrus.

Nb	Region to which cluster belongs to:	Z-MAX	Voxels	MNI coordinates X	Y	Z
Younger adults						
FA > HighCR (Z>2.3)						
1	medial SFG/dACC	4.59	2180	0	14	54
2	L frontal operculum (extending to IFG and insular cortex)	4.07	601	-46	16	0
3	R postcentral and precentral gyrus	4.53	557	44	-24	66
FA < HighCR (Z>3.1)						
1	R lingual gyrus (with intracalcarine cortex)	4.15	620	16	-74	4
2	L postcentral and precentral gyrus	3.88	156	-36	-28	54
Older adults						
FA < HighCR (Z>3.1)						
1	frontal pole and frontal medial cortex, extending to L dorsal caudate	4.18	762	4	62	0
2	R ventral caudate	4.09	204	20	-14	28
3	R lingual gyrus (with intracalcarine cortex and occipital fusiform gyrus)	3.77	193	14	-78	-12
4	R dorsal caudate	4.14	143	12	24	0

distinguishing two smaller clusters within: (1) R lingual gyrus, (2) L precentral and postcentral gyrus (see Table 2, Fig. 5B).

In older adults, a whole-brain analyses did not reveal FA-related increases compared to HighCR. But two very widespread clusters of FA-related decreases in activity were identified: (1) big cluster involving many areas from frontal pole to occipital pole, including, among others L postcentral and precentral areas, lateral occipital cortex, L paracingulate, posterior cingulate cortex, L precuneus, R lingual gyrus, subcortical areas (e.g. L thalamus, L putamen, L caudate and L hippocampus), and white matter, (2) cluster involving areas within R-sided: superior temporal gyrus (STG), postcentral and precentral gyrus, planum temporale, parietal and central operculum cortex, supramarginal gyrus, subcortical regions (R thalamus, R caudate, and R putamen) and white matter. Same as in the case of FA-decreases of brain activity in younger adults, the clusters extended beyond single or neighbouring anatomical areas (Table S1.1 and Fig. S1.1B in Supplementary Materials), thus, the primary threshold was increased to $Z > 3.1$ (Woo et al., 2014). It allowed for reporting four small clusters involving: (1) parts of frontal pole and frontal medial cortex (VMPFC), extending to L dorsal caudate, (2) R ventral caudate, (3) small area within R lingual gyrus with intracalcarine cortex and occipital fusiform gyrus, (4) R dorsal caudate (see Table 2, Fig. 5C).

In addition, a region of interest (ROI) analysis was conducted to test FA-related changes specifically in the hippocampus activity. To avoid selection bias, the ROIs in L and R hippocampus were defined using 75% probabilistic threshold of these regions as defined in the Harvard-Oxford Subcortical Atlas. One sample t-tests performed separately for younger and older adults revealed no significant FA-related changes in the activity of the L hippocampus, neither in younger adults ($p = 0.11$) nor in older adults ($p = 0.18$). Yet, there were significant FA-related changes in the R hippocampus in older adults ($t(23) = -2.27$, $p = 0.03$), and a trend in younger adults ($p = 0.08$). The percent signal change values were generally low (L hippocampus: YA M = -0.05, SE = 0.03; OA M= -0.03,

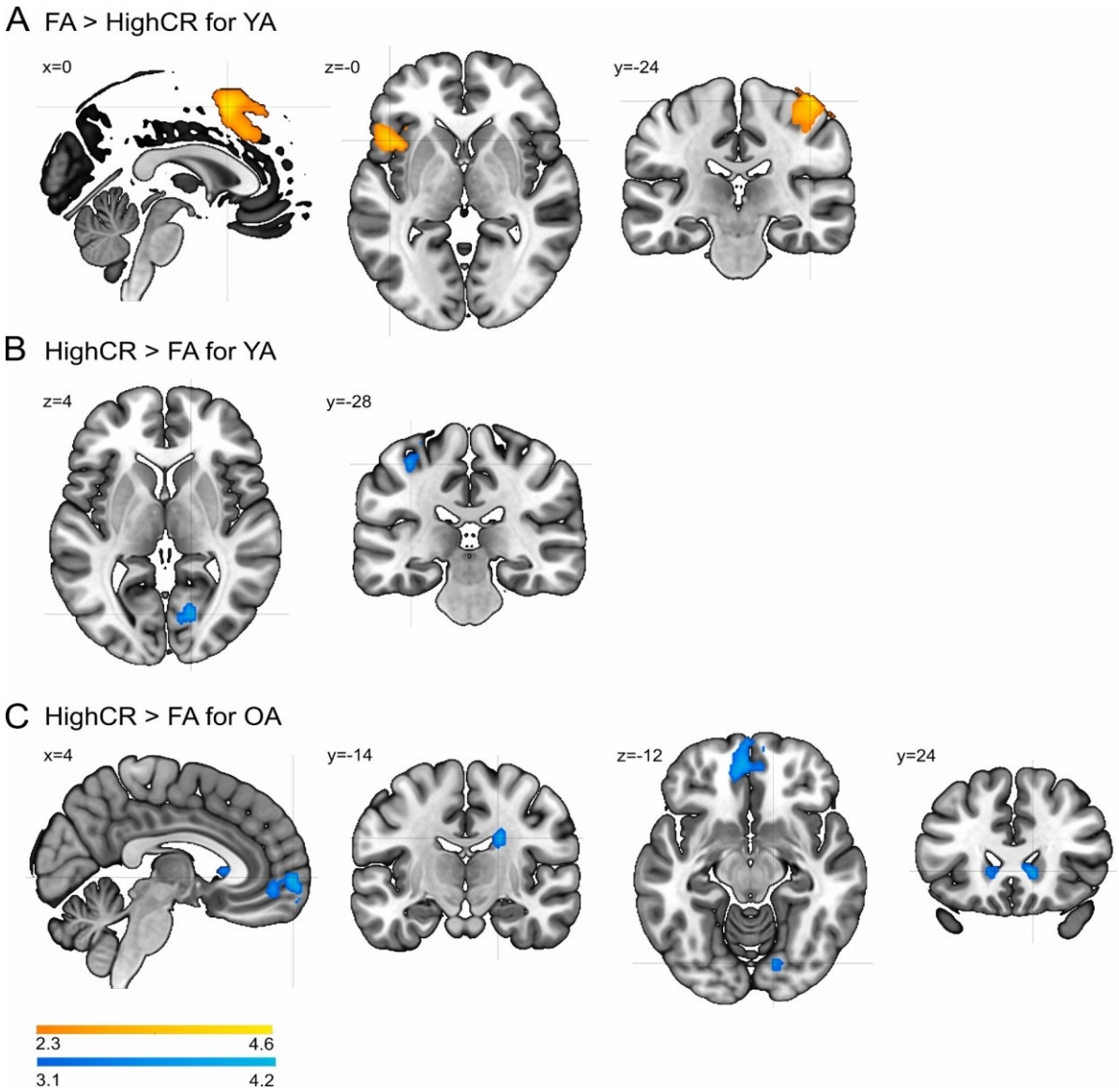

Fig. 5. A) False recognitions (FA)-related increases in brain activity in younger adults (YA). Three clusters: in medial superior frontal gyrus (mSFG), with local maxima also in dorsal anterior cingulate cortex (dACC); in left (L) frontal operculum (FO) extending to inferior frontal gyrus (IFG) and anterior insular cortex; and on the border of right (R) postcentral and precentral gyrus. B) FA-related decreases in brain activity in YA. Two clusters: in R lingual gyrus and in L postcentral and precentral gyrus. C) FA-related decreases in brain activity in older adults (OA). Four clusters: in frontal medial cortex and frontal pole; in R ventral caudate; in R lingual gyrus (frontal medial cortex also seen on a figure); and in R dorsal caudate (L dorsal caudate also seen on a figure). Clusters thresholded at $Z > 2.3$ in A and $Z > 3.1$ in B and C, $p_{corrected} < 0.05$.

$SE = 0.02$; R hippocampus: YA M = -0.05, $SE = 0.03$; OA M = -0.05, $SE = 0.02$) and with respect to R hippocampus only the SE (not the mean) was different between age groups. When the one-sample t-tests were conducted on all subjects across both age groups, there were significant differences in both L ($t(47)$ = -2.19, $p = 0.03$) and R hippocampus ($t(47)$ = -2.84, $p = 0.01$).

3.2.2. Age-differences in FA-related activity

To test the hypothesis that during false recognitions, younger adults, compared to older adults, exhibit increases in activity in frontal brain regions linked with performance monitoring and cognitive control, we performed whole-brain analyses with an unpaired two-sample t-test. The analysis revealed five clusters in which FA-related activity was higher for younger than for older adults: (1) involving R occipital pole and R lateral occipital cortex, (2) mSFG /ACC, (3) R frontal orbital cortex/frontal pole with parts of FO and insular cortex, and R IFG/ medial frontal gyrus (MFG), (4) L frontal pole (on borders with SFG/ MFG), (5) R precentral and postcentral gyrus (see Table 3, Fig. 6). No regions exhibited significant activation in the reverse contrast (i.e., OA > YA).

In addition, in order to answer our research question regarding the age-related differences in FA-related activity of the hippocampus, a ROI analysis was conducted. Unpaired t-tests performed separately for L and R hippocampus revealed no age-differences therein ($p = 0.74$ and $p = 0.91$, respectively).

3.2.3. Brain-behaviour interactions

Based on the hypothesis that the observed age-differences are associated with older adults' poorer ability to adjust their confidence judgements according to the response accuracy, a whole-brain analysis was performed with the metacognitive sensitivity index (*type two d',* see Fleming & Lau, 2014) as a covariate. When adjusted for participants'

Table 3
False recognitions (FA)–related increased activity in younger adults (YA), compared to older adults (OA). Peak activations for within each cluster, clusters thresholded at $Z > 2.3$, $p_{corrected} < 0.05$. L – left, R – right, dACC – dorsal anterior cingulate cortex, IFG – inferior frxontal gyrus, MFG – medial frontal gyrus, SFG – superior frontal gyrus.

Nb	Region to which cluster belongs to:	Z-MAX	Voxels	MNI coordinates X	Y	Z
Younger adults > older adults *(for FA > HighCR; Z>2.3)*						
1	R occipital pole and lateral occipital cortex	3.56	747	32	-86	-4
2	medial SFG/ dACC	3.4	627	8	16	54
3	R frontal orbital cortex/frontal pole with parts of frontal operculum and insular cortex; R IFG/MFG	3.55	625	46	24	-16
4	L frontal pole/ SFG/ MFG	3.29	595	-28	46	22
5	R precentral gyrus and postcentral gyrus	3.91	584	46	-22	64

ability to calibrate their confidence judgements, only one cluster in R occipital region survived the significance threshold in the age-groups comparison of FA-related activity (see Table 4, Fig. 7A), suggesting that this is the only structure presenting age-related differences in activity, independently of confidence level. Importantly, no simple effects of metamemory ability nor the impact of age and metamemory interaction were observed.

In addition, in order to test whether the observed between-groups differences are impacted by participants' differences in memory performance, the whole-brain analysis was performed with the sensitivity index (d', see Macmillan & Creelman, 2004) as a covariate. In contrast to the impact of metamemory abilities and even though there was no significant between-group effect in performance at the behavioural level, introducing d-prime as covariate strengthened the age-related differences in FA-related brain activity. Activities within visual and frontal cortex became more widespread and bilateral (e.g. separate clusters were found in L MFG and L visual cortex), and the size of clusters involving mSFG/ACC and FO increased (see Table 4, Fig. 7B). In addition, better memory abilities corresponded with increased FA-related activity in the ACC across age groups (see Table 4, Fig. 7C). No interaction between age and sensitivity was observed.

Furthermore, to test whether the age-related differences in brain activity are affected by the RT (as older adults had higher probe RT than younger adults), models with Δ probe RT and Δ confidence RT (i.e. RT measured as difference in individuals' mean RT for FA and HighCRs) were tested by adding the respective covariates to regressors' matrix. The age-related differences adjusted for Δ probe RT or Δ confidence RT were very similar to the ones observed when adjusted for d-prime or with no covariate (see Table S1.2 and Fig. S1.2 in Supplementary Materials, and Table 4 and Fig. 8, respectively). Simple across-groups effects of Δ probe RT and Δ confidence RT were not observed, similarly like the interaction between age and Δ confidence RT. However, an interaction effect of age and Δ probe RT was observed. In 3 clusters the slope between brain activity and Δ probe RT was larger for older than younger adults: (1) region within R MFG extending to SFG, R frontal pole, (2) R angular gyrus extending to lateral occipital cortex and middle temporal gyrus, and (3) medial precentral gyrus/supplementary motor cortex (SMC; see Table 4, Fig. 8). A post-hoc analysis of individual group slopes within each of these clusters indicated negative effects of Δ probe RT on FA-related brain activity in younger adults (see Table S1.2 in Supplementary Materials), whereas no effects were significant in older adults. Thus, for younger adults, the longer the individuals' FA-related increase in probe RT (compared to HighCR), the lower the FA-related activity in these regions. Importantly, clusters with the interaction

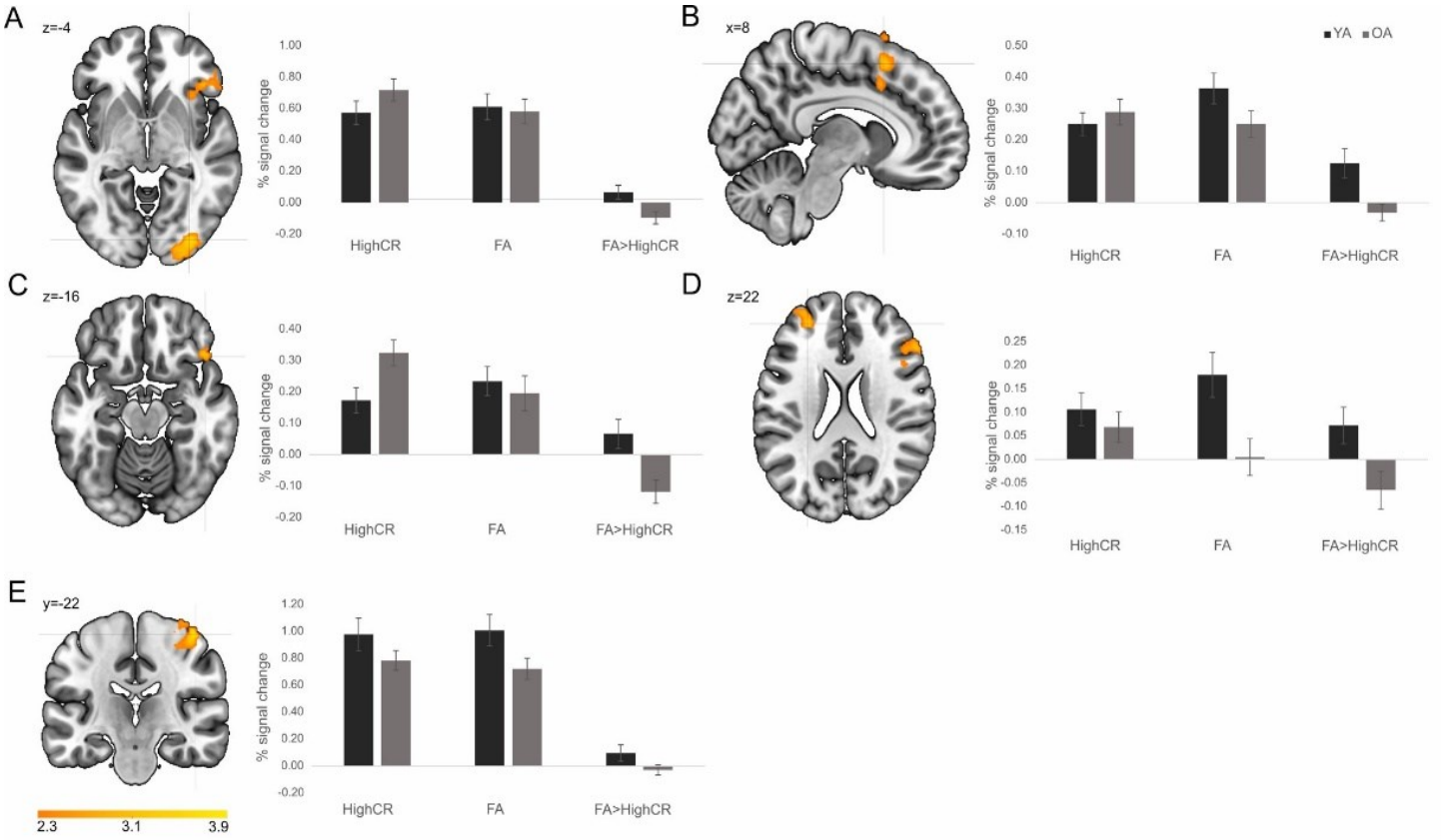

Fig. 6. Age-related differences in false recognitions of lures (FA)-related activity. Increased activity in younger adults (YA), compared to older adults (OA), in five clusters: A) visual cortex, B) medial superior frontal gyrus/anterior cingulate cortex (mSFG/ACC), C) right (R) frontal orbital cortex/frontal pole with parts of frontal operculum (FO) and insular cortex, and R inferior frontal gyrus/medial frontal gyrus (IFG/MFG), D) left (L) frontal pole extending to the borders of SFG/MFG, and D) R precentral and postcentral gyrus. Graphs depict mean % signal change for each cluster for YA and OA adults for highly confident correct rejections of lures (HighCR) > implicit baseline, FA > implicit baseline, FA >HighCR. Clusters thresholded at $Z > 2.3$, $p_{corrected} < 0.05$.

Table 4

False recognitions (FA)–related increased activity in younger adults (YA), compared to older adults (OA) when adjusted for type 2 d', d' and Δ confidence reaction time (RT); the positive effect of d' across both age group; and an interaction effect of age and Δ probe RT on FA–related activity. Peak activations for within each cluster, clusters thresholded at $Z > 2.3$, $p_{corrected} < 0.05$. L – left, R – right, dACC – dorsal anterior cingulate cortex, IFG – inferior frontal gyrus, MFG – medial frontal gyrus, SFG – superior frontal gyrus.

Nb	Region to which cluster belongs to:	Z-MAX	Voxels	MNI coordinates X	Y	Z
Younger adults > older adults adjusted for type 2 d' (Z>2.3)						
1	R occipital pole and lateral occipital cortex	3.88	617	34	-88	-4
Younger adults > older adults adjusted for d' (Z>2.3)						
1	medial SFG/ dACC	3.91	1553	-6	22	40
2	L frontal pole (on boarders with SFG)	4	1301	-28	46	22
3	R frontal orbital cortex/frontal pole with parts of frontal operculum and insular cortex; R IFG/MFG	4.28	1124	46	26	-16
4	R occipital pole and lateral occipital cortex	4.07	909	34	-86	-4
5	R cerebellum	3.48	752	38	-58	-38
6	L occipital pole and lateral occipital cortex	3.22	633	-18	-100	-2
7	L MFG	3.51	618	-44	26	42
8	R precentral gyrus and postcentral gyrus	4.3	527	46	-22	64
Positive effect of d' across both age groups (Z>2.3)						
1	ACC/ medial SFG	3.77	845	0	40	22
Interaction between age and Δ probe RT (Z>2.3)						
1	R MFG extending to SFG, R frontal pole	3.48	819	36	18	60
2	R angular gyrus extending to lateral occipital cortex and middle temporal gyrus	3.02	671	50	-54	34
3	medial precentral gyrus/ supplementary motor cortex	3.38	500	-8	-14	64
Younger adults > older adults adjusted for Δ confidence RT (Z>2.3)						
1	R precentral gyrus and poscentral gyrus, medial SFG/dACC, L frontal pole (on boarders with SFG/MFG)	4.32	2748	44	-22	64
2	R occipital pole and lateral occipital cortex	4.11	891	26	-98	-2
3	R frontal orbital cortex/frontal pole with parts of frontal operculum and insular cortex; R IFG/MFG	3.84	818	46	24	-16
4	R cerebellum	3.51	554	16	-86	-42

effect of age and probe RT on FA-related activity are not overlapping with clusters of the age-differences in FA-related activity (see Table 3).

4.Discussion

In this study we aimed to investigate the neural mechanisms underlying false recognitions in visual STM in younger and older adults. Additionally, we tested whether the main behavioural results replicate the ones reported in our previous STM study (Sikora-Wachowicz et al., 2019). The main findings are discussed below.

4.1. Age-related differences in confidence following false memory decisions, but not in false recognitions rate

On the behavioural level, the general pattern of results replicates the one from our previous experiment (Sikora-Wachowicz et al., 2019).

Namely, older adults are more confident of their false recognition than young adults, although the rate of false alarms is comparable in both age groups.

Albeit the procedure was effective in eliciting perceptually-based false recognitions (as indicated by analyses of *d'* values and error rates for lure probes, see Fig. 2 and Table 1, respectively), we did not observe age-differences in accuracy, neither as measured by *d'* nor in the rate of false recognitions. Moreover, the results of the Bayesian t-test on FA-rates provided moderate support for lack of age-differences therein. This contrast results of episodic memory studies, indicating older adults' higher susceptibility to false recognitions, linked with the senescence-related changes in associative and monitoring processes (see Devitt & Schacter, 2016). One possible explanation for this observation is that avoiding false alarms in item-based STM rely on intra-item visual feature binding, that seems to remain relatively intact with aging (e.g. Brown et al., 2017; Peterson & Naveh-Benjamin, 2016; Rhodes et al., 2017; Rhodes et al., 2016).

There is a possibility that the properties of the task could have attenuated observed age-differences (see also Sikora-Wachowicz et al., 2019). While age-differences in long-term memory performance were consistently observed across different types of tasks, and different types and numbers of stimuli in a set, the effect was modulated by task characteristics, e.g., lower for pictures than words (see the meta-analysis of Fraundorf et al., 2019), and for abstract than concrete objects (Koutstaal et al., 2003; Pidgeon and Morcom, 2014). Furthermore, although some studies indicated older adults' increased susceptibility to false alarms was linked with perceptual but not conceptual relatedness of words (e.g, Ly, Murray, & Yassa, 2013), in general, it seems to be more robust in case of conceptually- than perceptually related stimuli (e.g., Koutstaal et al., 2003; Pidgeon and Morcom, 2014; see also Fraundorf et al., 2019). In addition, some findings suggest that increasing the set size at encoding particularly affects the OA' FA rate (e.g., Pidgeon & Morcom, 2014). Importantly, the meta-analyses of Fraundorf et al. (2019) did not confirm the effect of this variable on the age-differences in susceptibility to false alarms.

Finally, it is also possible that in an LTM version of our task, older adults' performance would also be preserved. Importantly, although some studies have reported comparable performance of YA and OA in LTM (e.g., error rates in a hybrid visual and LTM memory search task, see Wiegand & Wolfe, 2020), to date, no known variable was identified which would consequently lead to such results (see Fraundorf et al., 2019). Importantly, in some cases, even if the performance was found to be well preserved with age, there were still some effects of age linked with the interference from associative lures (see Wiegand & Wolfe, 2020). Also, some findings suggest that OA, compared to YA, may not present increased FA rate for single abstract objects (Koutstaal et al., 2003; Pidgeon and Morcom, 2014). Yet, the studies, using the same experimental task and material, involved incidental encoding which could possibly affect YA' inflated FA rate for single abstract objects (see Koutstaal et al., 2003). Also, variance in performance was high, and FA rate very low (when corrected for foils, the rates were around zero; see Pidgeon & Morcom, 2014). Finally, corrected false recognition rates could potentially reduce age-differences related to more general FA-related processes observed also in FA to the novel category lures (see also Fraundorf et al., 2019). Taken together, we would assume that age-differences in FA rate would occur in an LTM version of our task, especially given the high rate of perceptually-related FA and the potentially higher impact of hippocampally-mediated binding on LTM performance. Yet, future studies are needed to support these assumptions.

Importantly, older adults, compared to younger ones, presented poorer abilities to adequately adjust their confidence level regarding the response accuracy; they had higher confidence in their false recognitions. These results are in line with the findings from the episodic memory literature (e.g., Dodson, Bawa, & Krueger, 2007; Dodson et al., 2015; Fandakova et al., 2013b; Shing et al., 2009). Hyper-binding,

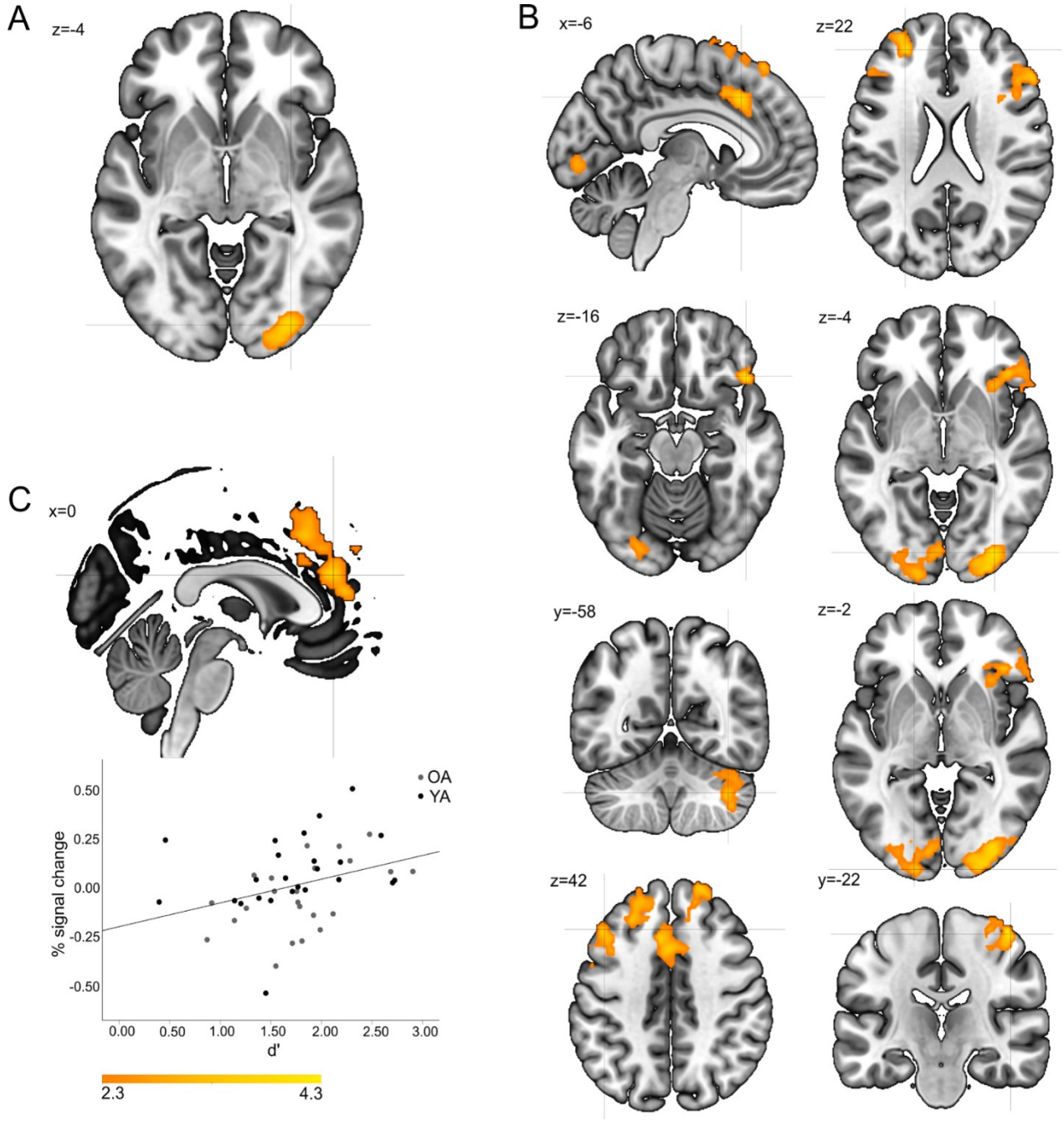

Fig. 7. Age-related differences in false recognitions (FA)-related activity when adjusted for A) type 2 d' as a covariate – one cluster in the visual cortex, and B) d' – eight clusters as depicted in Table 4. C) A positive effect of *d'* across both age groups. Chart depicts a relationship between each subject's mean % signal change in anterior cingulate cortex (ACC) for FA > highly confident correct rejections of lures (HighCR) and his/hers *d'*. Clusters thresholded at $\mathbb{Z} > 2.3$, $p_{corrected} < 0.05$.

resulting from impaired pattern separation, was proposed as one of the possible explanations of older adults' high confidence episodic false recognitions (e.g., Dodson, Bawa, & Krueger, 2007; Shing et al., 2011, 2009). However, if older adults' higher confidence in FA resulted from their higher susceptibility to misrecollections, one would also expect higher FA rate in this age group. Therefore, this mechanism is not likely to explain our findings. Instead, our results suggest that older adults' high-confidence errors in item-based STM may stem from monitoring impairments - other mechanism that has been suggested to contribute to age-differences in high-confidence false alarms in episodic memory (Fandakova et al., 2013a, 2013b). First, we observed age-differences not only in confidence after FAs but also in the metacognitive sensitivity index – *type 2 d'* – serving as a more general measure involving all probe types. Second, executive functioning and top-down control, crucial for working memory performance (Gazzaley & Nobre, 2012), undergo age-related impairments (Gazzaley et al., 2005; Sander et al., 2012). In turn, they may contribute to older adults' feeling of correctness when making an error. Accordingly, older adults' high-confidence (or 'remember') errors have been linked with lower executive functioning (e.g. Fandakova et al., 2013b; McCabe et al., 2009), and age-differences in episodic false memories were also linked with impairments in error monitoring and uncertainty processing (Fandakova, Sander, et al., 2019).

Additionally, our RT analyses showed that, despite older adults needing more time to make a 'same-different' decision than younger adults, both age groups needed more time to make false recognitions that to correctly reject a lure, and to make confidence decisions after FA than after correct rejection. The results suggest that both age groups process the information in a similar manner, presenting calibrated monitoring engagement, stronger when memory details are diminished. Therefore, it may imply that the observed age-differences in confidence level result rather from older adults' less efficient monitoring of retrieval details and uncertainty signals.

4.2. Age-differences in FA-related activity of brain regions linked with monitoring and uncertainty processing

At the neural level, age-related differences were observed in brain

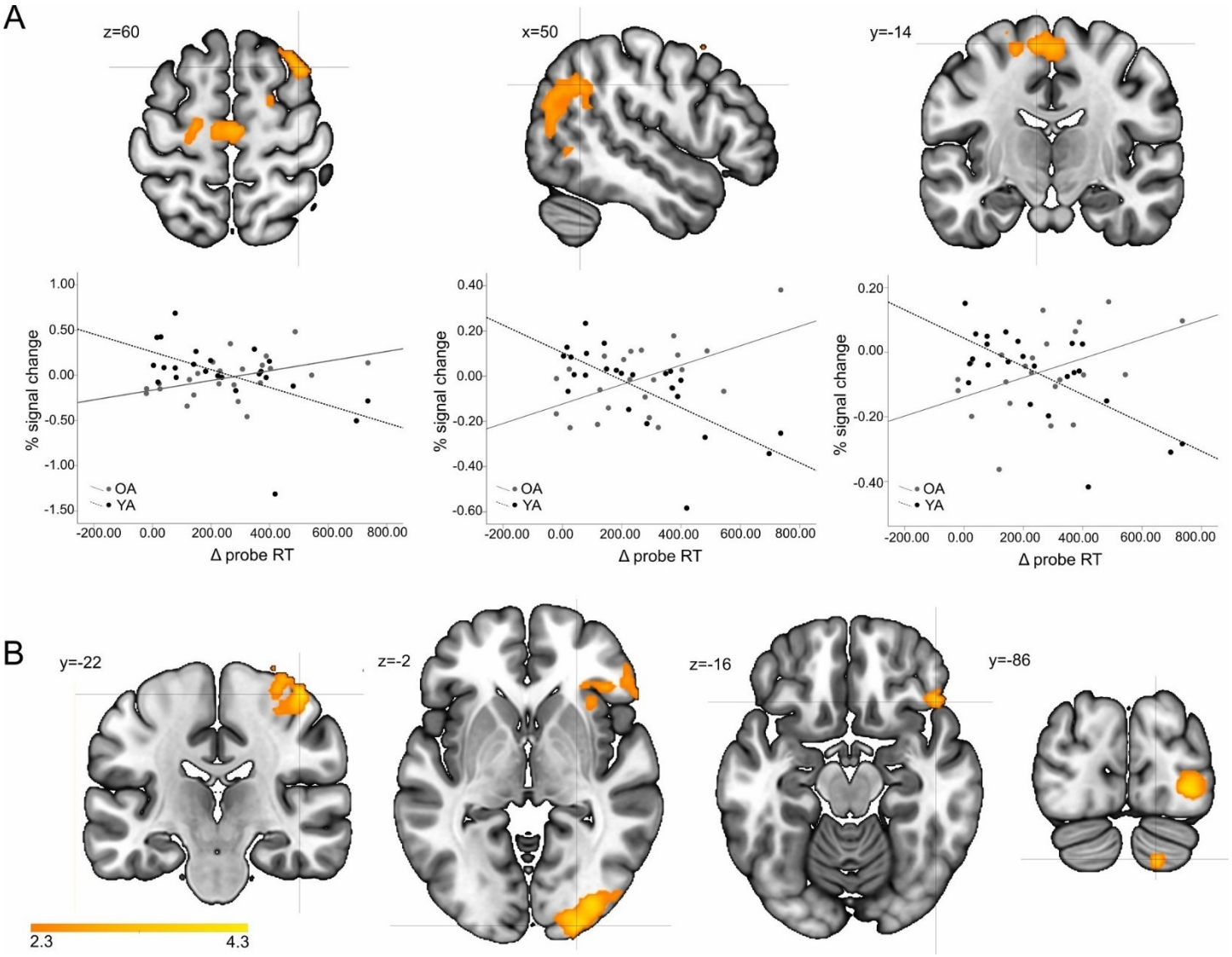

Fig. 8. A) Interaction between age and Δ probe reaction time (RT). Charts depict an interaction effect in three consecutive clusters. B) Age-related differences in false recognitions (FA)-related activity when adjusted for Δ confidence RT. Clusters thresholded at $Z > 2.3$, $p_{corrected} < 0.05$.

regions linked with performance/error monitoring and processing of representations in working memory, but not in the hippocampus.

In line with our hypothesis, FA-related increases in brain activity were observed only in younger adults, primarily in mSFG/dACC and in the L FO/AI. These regions were previously associated with monitoring processes, in particular with evaluation of errors and uncertainty signals (Botvinick et al., 2004; Carter & van Veen, 2007; Fleming & Dolan, 2012; Neta et al., 2014). This suggests that younger, but not necessarily older adults were able to detect and evaluate FA-related error and ambiguity signals. These results are consistent with recent findings of an episodic memory study, indicating that only younger adults were able to modulate the recruitment of this cingulo-opercular region for FAs and low-quality CRs, compared to high-quality CRs (Fandakova, Sander, et al., 2018). Importantly, in a direct age-groups comparison, we observed higher FA-related activity for younger compared to older adults in the cingulo-opercular region (dACC and FO/AI), as well as in parts of prefrontal cortex linked with performance monitoring and cognitive control (lateral frontal pole, MFG, and parts of IFG). The lateral frontal pole corresponds with the APFC, and the age-related changes in its recruitment were associated with susceptibility to false alarms and impairments in metamemory assessments (e.g. Fandakova, Bunge, et al., 2018; Fandakova et al., 2014; 2015). Furthermore, the frontal clusters found in our age-comparison involve parts of the VLPFC (IFG) - linked with inhibitory control and proactive interference during processing lures in STM (Atkins & Reuter-Lorenz, 2011), as well as DLPFC (MFG) - linked with age-differences in cognitive control. These findings correspond with studies showing that in episodic memory, older adults' highly confident FAs are linked with impairments in frontal lobe functioning (Fandakova et al., 2013b), as well as with the ones regarding senescent-related impairments of the modulated DLPFC recruitment (McDonough et al., 2013).

In addition, in older adults robust FA-related decreases were present in the VMPFC extending to the frontal pole and the caudate. While VMPFC was linked with adequacy of confidence judgements (Hebscher & Gilboa, 2016) and older adults' compensation in this area was associated with improvement of memory-dependent choices (Lighthall et al., 2014), the interaction between PFC and basal ganglia (especially dorsal caudate) was linked with efficient top-down control of working memory representations (for review see Sander et al., 2012; see also Huang et al., 2017). The caudate activity was also found to be increased for difficult recall-to-reject decisions when compared to false recognitions (see Kurkela & Dennis, 2016), suggesting that correct rejections were challenging for older adults. Taken together, it also implies that older adults' higher FA-related confidence is linked with their impairments in monitoring and top-down control.

It is known that frontal brain regions interact with more posterior ones, e.g., during processing sensory representations of memorized items. Consistently, older adults' impairments were shown in the interplay between prefrontally-mediated top-down control and low- level feature binding mediated by posterior brain regions (see Sander

et al., 2012). For instance, in the episodic memory older adults exhibited FA-related decreases in the activity of not only prefrontal, but also the parahippocampal and occipitotemporal regions, linked with reduced retrieval of details and diminished reliance on reconstruction processes (Dennis et al., 2014, Dennis et al., 2014). While in the present experiment both age groups presented widespread FA-related decreases, e.g., in the lingual gyrus at lower threshold extending to other visual areas, in a direct between groups comparison, the FA-related activity in visual cortex was lower for older adults. Accordingly, visual cortex was linked with sensory reactivation of previously seen stimuli (Slotnick & Schacter, 2004, 2006) and imagery retrieval of memorized information (Dennis et al., 2014, Dennis et al., 2014).

Importantly, we did not find any age-differences in hippocampal activity, even in the ROI analysis ($p > 0.74$). In the context of episodic memory, hippocampal volumetric decreases were linked with older adults' higher susceptibility to FAs (Shing et al., 2011). Likewise, age-related hippocampal impairments have been suggested as a potential cause of older adults' higher FA-related confidence (so-called 'illusory recollections', see Dodson, Bawa, & Krueger, 2007; Shing et al., 2009). Age-related differences in hippocampal binding were observed also in the context of working memory (e.g. Mitchell et al., 2000). However, several studies suggest that in STM, the hippocampus is involved in memorizing conjunctions rather than separate items (Hannula et al., 2006; Olson et al., 2006), or that it is involved when the material is sufficiently complex and requires high-resolution binding (Yonelinas, 2013). In our study, we observed significant FA-related changes in the activity of older adults' right hippocampus, and a similar non-significant trend in younger adults. Percent signal change values were generally low, yet FA-related changes in both left and right hippocampus were identified in a whole group analysis. This suggests that in our item-based visual STM task with single yet complex abstract objects as targets, the impact of the hippocampus on mediating FA is present but rather difficult to reveal. It corresponds well with the findings regarding intra-item visual feature binding being relatively intact with aging (e.g. Brown et al., 2017; Rhodes et al., 2016) and shed a light on a comparable FA rate in our experiment.

Importantly, when age-differences were adjusted for *type 2 d'* as a covariate, only activity of the visual cortex was differentiating younger and older adults. It suggests that it is the only area which changes with age independently of confidence, whereas the differences in the cingulo-opercular region and parts of PFC are at least partially linked with efficient postretrieval monitoring. These results are in line with our hypothesis that age-differences in FA-related frontal activity are associated with older adults' poorer metacognitive abilities.

A lack of a simple effect of *type 2 d'* across age groups and the absence of an interaction effect of *type 2 d'* and age may seem surprising. However, it should be noted that frontal brain regions, such as the APFC and DLPFC, are linked not only with decisions to report uncertainty and postretrieval assessment (Fandakova, Bunge, et al., 2018; Fleming & Dolan, 2012), but also with performance-related monitoring and control (Edin et al., 2009; Fandakova et al., 2014; Gazzaley & Nobre, 2012). In our experiment, when accounting for individual differences in memory performance (*d'*), the observed age-differences in FA-related activity become more widespread and bilateral, both in visual and frontal areas. Consistently, previous findings indicated that brain activity in memory tasks is related to performance level (e.g. Nagel et al., 2009; Fandakova, Sander, et al., 2018). For instance, highly functioning older adults, when compared to low performing, presented increased activity in the MFG for CRs, a pattern similar to the one in younger individuals (Fandakova et al., 2015). Also, older adults' more bilateral recruitment of frontal brain regions (including the DLPFC and APFC) was suggested to play a compensatory role in working memory performance (Rajah & D'Esposito, 2005; Reuter-Lorenz et al., 2000). Taken together, the results may suggest that whereas the FA-related activity in the aforementioned regions was, in general, higher for younger adults, older adults' with higher *d'* could have engaged them more (e.g. present more 'youth-like' activity pattern) to achieve good discrimination between targets and lures.

Additionally, despite the observed age-differences in the dACC/mSFG activity, the positive effect of *d'* was found in the ACC across both age groups, indicating that better memory performance was linked with increased FA-related ACC activity irrespective of age. It is in line with the previous studies showing that the link between ACC activity and performance is stable across adulthood (de Chastelaine et al., 2016). For instance, Fandakova, Bunge, et al. (2018, Fandakova, Sander, et al., 2018) showed that despite the age-differences in the modulation of the cingulo-opercular activity regarding the memory quality, in both age groups it predicted the performance level (namely, susceptibility to false alarms). Consistently, in our task the ACC activity supports performance monitoring irrespective of age, although it is also less efficient in older adults, potentially contributing to the observed age-related differences in postretrieval assessments.

Finally, as reaction time may affect activity of such brain regions as the ACC and FO (Neta et al., 2014), we tested its impact on age-differences in FA-related activity. The results showed that, despite no effects of age on the behavioural level, individual variability in confidence RT attenuates age-differences in FA-related brain activity, particularly in the cingulo-opercular circuit. It is likely that not only younger adults but also older adults with higher Δ confidence RT present stronger involvement of aforementioned regions for slow and more ambiguous FAs (see Neta et al., 2014). Furthermore, an interaction effect of age and Δ probe RT was observed within parts of frontal lobe and in angular gyrus (extending to neighbouring occipital and temporal areas). As indicated by the post-hoc test, the significant effect was only in younger adults: the longer the FA-related increases in probe RT, the lower the activity. These regions are linked with recognition and processing representations in working memory, and undergo senescence- related changes (for review see e.g. Sander et al., 2012). It may suggest that in our task younger adults' retrieval problems are associated with increased response time, potentially due to increased monitoring demands. Importantly, significant clusters observed in this analysis did not overlap with the ones identified in the analysis of age-differences in FA-related activity. Potentially, it might correspond to the previous distinction between two task control areas: frontoparietal regions (where error-related differences occur during evidence accumulation) and cingulo-opercular ones (differences occurring later, when the decision is made; see Neta et al., 2014; Ploran et al., 2007). However, most importantly, it also indicates that the observed age-differences in FA-related brain activity, being of main interest in the current study, can be interpreted despite the presence of the interaction effect of RT and age on BOLD activity.

4.3. Age-differences in the FA-related brain activity: The impact of contrast choice

It is noteworthy that when the FA-related brain activity was tested in the HighHit contrast (see Section 3 in Supplementary Materials), both age groups presented FA-related increases in the ACC-FO/AI activity (more robust and bilateral in YA, left side only in OA), and in the parietal cortex. In YA there were also FA-related increases in the lateral prefrontal cortex. Importantly, in a direct age-group comparison there were no significant age-differences in the cingulo-opercular circuit and in the R IFG/MFG (although the ones in the L APFC were present in both FA-HighCR and FA-HighHit contrasts, and the ones in the visual cortex became more widespread in the contrast with HighHit). Yet, age-differences in the ACC activity were significant after controlling for *d'*, probe RT, and confidence RT (see Neta et al., 2014). In addition, the FA-related decreases in the brain activity seemed to be less extensive in the FA-HighHit contrast, and there were no significant FA-related changes in the hippocampal activity in the ROI analyses, as well as no significant age-differences therein.

As already mentioned, the contrast-dependent variations in the

activity of the cingulo-opercular and frontoparietal regions may result from the fact that the Hit-based contrast does not control for the increases in monitoring and cognitive control linked with processing of lures in general. Also, it seems that in our task, HighCR responses required both detailed memory representations of targets as well as efficient monitoring and control over these representations, whereas HighHit responses only required general familiarity. Consequently, one might expect that FA-related increases in brain regions linked with monitoring and cognitive control would be higher when FAs are contrasted with Hits rather than CRs (for the contrast dependent variations in the ACC activity see Kurkela & Dennis, 2016). The lack of control for processes linked with lures in general, may also shed a light on the selective presence of a positive effect of type 2 d' in the parietal cortex only in the FA-HighHit contrast. Namely, in the CR-based contrast this effect might be attenuated as the parietal cortex activity is not only linked with confidence processing (e.g., Chen et al., 2013), but, due to its involvement in processing of WM representations within the frontoparietal cognitive control network, it is likely to be increased for lures in general. In turn, in the contrast of false recognitions versus true recognitions, some of the recognition related brain activity can be removed by the contrast, potentially influencing the FA-related decreases in the recognition–related areas (see Kurkela & Dennis, 2016). This removal of the recognition-related processes in the HighHit-based contrast might also shed a light on the lack of significant FA-related decreases in the hippocampus activity in this contrast. Yet, the contrast dependent variations in hippocampal activity can be also modulated by the fact that the detailed recollection is required for HighCR, but not necessary in HighHit.

Importantly, as older adults tend to over-rely on familiarity (Devitt & Schacter, 2016), in our task the FA-related brain activity in this age group can be disproportionally affected in the Hit-based contrast. Importantly, the results of a comparison of the brain activity during HighCR versus HigHits (see Section 4 in Supplementary Materials) are in line with this assumption, indicating that in both age groups there are widespread HighCR-related increases in the brain activity (e.g., in the lateral prefrontal and parietal regions), but within the mSFG/dACC, bilateral FO/AI and parts of R IFG/MFG the increases in activity are higher in OA than in YA. Thus, while both age groups present increased cognitive control during HighCR, in OA the discrepancy in the involvement of these processes between HighCR and HighHit is higher. These results may shed a light on the attenuated age-differences in the FA-related activity of the ACC and parts of the R IFG/MFG selectively in the HighHit contrast. Namely, they may suggest that both age groups present increased monitoring of lures, whereas only YA recruited additional monitoring processes specifically linked with false recognitions. From a broader perspective, this could imply that age-differences in processes specifically linked with FAs are better reflected in the HighCR contrast. Yet, future analyses would be needed to test these possibilities.

5. Conclusions

To summarize our most important findings, we did not observe age- differences in FA rate nor in hippocampal activity, but older adults presented higher confidence accompanying FAs and lower activity in prefrontal and cingulo-opercular brain regions linked with monitoring and uncertainty processing. Moreover, these age-differences in frontal activity were influenced by participants' metacognitive abilities, when added to an analysis as a covariate. These results are important in the context of previous episodic memory findings, suggesting that older adults' greater susceptibility to false alarms and highly confident false alarms results from their hippocampally-mediated binding impairments (Dodson, Bawa, & Krueger, 2007; Shing et al., 2011), and changes in the monitoring abilities linked with functioning of the prefrontal cortex and the cingulo-opercular region (Fandakova et al., 2013b; Fandakova, Sander, et al., 2018). The current findings suggest that in an item-based visual STM, the age-related differences in confidence following false recognitions are underlain by differences in monitoring abilities and cognitive control, rather than binding impairments (see also Sikora- Wachowicz et al., 2019).

In addition, as there is a limited number of studies on short-term false recognitions, and only few of them, conducted on younger participants, investigated the neural mechanisms (Atkins & Reuter-Lorenz, 2011; Iidaka et al., 2014), our results provide new knowledge on false recognitions in general. First, brain regions involved in visual false memories in STM seem to be largely overlapping with the ones linked with false recognitions in the episodic memory (for a quantitative meta-analysis see Kurkela & Dennis, 2016). Second, in our STM study the age-differences occurred in confidence level (similarly to episodic memory studies) but not in FA rate, suggesting that there might be some common and some unique mechanisms influencing FA at short and long term. It was also suggested by Flegal and Reuter-Lorenz (2014), who showed that in younger adults processing depth may differently influence the rate of long- and short-term false memories, but not the related subjective confidence. Taken together, the obtained results may, to some extent, challenge the traditional dichotomy of short- and long-term memory processes. Yet, further studies are needed to test these assumptions on the neural level, especially ones manipulating material type and number of stimuli in a set, as well as directly comparing age-differences in confident false recognitions occurring at short and long lag.

To conclude, the present study provides initial insights in the neural mechanisms underlying false recognition in short-term memory using an item-based visual STM task. In particular, it broadens the knowledge about the mechanisms underlying older adults' high confidence false recognitions in STM, highlighting the role of the prefrontal cortex and the cingulo-opercular circuit in their occurrence.

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CRediT authorship contribution statement

B. Sikora-Wachowicz: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing - original draft, Writing - review & editing. **A. Keresztes:** Conceptualization, Methodology, Supervision, Writing - review & editing. **M. Werkle-Bergner:** Conceptualization, Methodology, Supervision, Writing - review & editing. **K. Lewandowska:** Conceptualization, Methodology, Writing - review & editing. **T. Marek:** Conceptualization, Methodology, Supervision, Writing - review & editing. **M. Fafrowicz:** Conceptualization, Funding acquisition, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://hdl.handle.net/21.11116/0000-0008-3F4F-B.

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