Routledge
Taylor & Francis Group

Aging, Neuropsychology, and Cognition

A Journal on Normal and Dysfunctional Development

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/nanc20

Shared vivid remembering: age-related differences in across-participants similarity of neural representations during encoding and retrieval

Adrien Folville, Mohamed Ali Bahri, Emma Delhaye, Eric Salmon & Christine Bastin

To cite this article: Adrien Folville, Mohamed Ali Bahri, Emma Delhaye, Eric Salmon & Christine Bastin (2022) Shared vivid remembering: age-related differences in across-participants similarity of neural representations during encoding and retrieval, Aging, Neuropsychology, and Cognition, 29:3, 526-551, DOI: 10.1080/13825585.2022.2036683

To link to this article: https://doi.org/10.1080/13825585.2022.2036683

AGING, NEUROPSYCHOLOGY, AND COGNITION
2022, VOL. 29, NO. 3, 526–551
https://doi.org/10.1080/13825585.2022.2036683

Shared vivid remembering: age-related differences in across-participants similarity of neural representations during encoding and retrieval

Adrien Folville[a,b], Mohamed Ali Bahri[a], Emma Delhaye[a,b,c], Eric Salmon[a,b] and Christine Bastin[a,b]

[a]GIGA-CRC in Vivo Imaging, University of Liège, Liège, Belgium; [b]Department of Psychology, Psychology and Neuroscience of Cognition Research Unit, University of Liège, Liège, Belgium; [c]Faculdade de Psicologia, CICPSI, Universidade de Lisboa, Lisbon, Portugal

ABSTRACT

Recent advances in multivariate neuroimaging analyses have made possible the examination of the similarity of the neural patterns of activations measured across participants, but it has not been investigated yet whether such measure is age-sensitive. Here, in the scanner, young and older participants viewed scene pictures associated with labels. At test, participants were presented with the labels and were asked to recollect the associated picture. We used Pattern Similarity Analyses by which we compared patterns of neural activation during the encoding or the remembering of each picture of one participant with the averaged pattern of activation across the remaining participants. Results revealed that across-participants neural similarity was higher in young than in older adults in distributed occipital, temporal and parietal areas during encoding and retrieval. These findings demonstrate that an age-related reduction in specificity of neural activation is also evident when the similarity of neural representations is examined across participants.

ARTICLE HISTORY
Received 27 May 2021
Accepted 27 January 2022

KEYWORDS
Episodic memory; aging; pattern similarity; shared memory; fMRI

Introduction

For years, cognitive neuroscience has studied episodic memory as an idiosyncratic process, whereby individuals encode and retrieve spatio-temporal contextual details and specific features from their past (Johnson et al., 1993; Tulving, 1972). But considering that humans are social beings, a growing number of studies have begun to examine how neural representations of memory events were shared across individuals (Chen et al., 2017; Koch et al., 2020; Oedekoven et al., 2017; Zadbood et al., 2017). By means of recent multivariate fMRI analyses, existing studies have revealed shared neural representations underlying memory content in posteromedial brain regions both during memory encoding and retrieval, thus suggesting that episodic memory mechanisms may function in a similar way across individuals (Chen et al., 2017; Koch et al., 2020; Xiao et al., 2020). It is now well-established that healthy aging reduces the specificity of the neural representations of visual stimuli, which may account, at least to some extent, for the age-related

CONTACT Christine Bastin christine.bastin@uliege.be
Supplemental data for this article can be accessed here.

episodic memory decline (Koen & Rugg, 2019; Koen et al., 2020; Zheng et al., 2018). Previous studies have examined age-related differences in the specificity of neural representations by examining the similarity of brain patterns of activations within-participants (e.g., the repeated processing of a scene by the same participant), but whether aging affects across-participants similarity of neural representations (e.g., the processing of the same scene by different participants) is a question that has yet to be examined. Here, we used multivariate Pattern Similarity Analyses (PSA) to examine age-related changes in across-participants similarity of neural patterns of activations during the encoding and the retrieval of vivid memories.

Age-related reductions in the precision of episodic memory retrieval have been well-documented, with studies showing that older adults have difficulties in recollecting contextual details from the remembered episode (Bayen & Murnane, 1996; Cansino, 2009; Mitchell & Johnson, 2009; Schacter et al., 1991). Normal aging is also associated with a decline in the capacity to remember specific episodic memory details (Addis et al., 2010; Levine et al., 2002; Piolino et al., 2010; St. Jacques & Levine, 2007). Somewhat surprisingly, a sizable number of previous studies have reported that older adults subjectively judge the quality (e.g., the vividness) of their memories as being at least as high as young adults (Abram et al., 2014; Comblain et al., 2005; Rubin & Schulkind, 1997; Schlagman et al., 2009). What makes this observation even more striking is that it was also reported in studies showing an age-related reduction in the level of richness of episodic memory content (Folville, D'Argembeau et al., 2020; Hashtroudi et al., 1990; Robin & Moscovitch, 2017), thus suggesting that subjective vividness ratings may not index the richness of older adults' recollective experiences (see, Folville, Simons et al., in press for a review). Consistently, studies directly relating subjective memory vividness with an objective measure of the richness of memory across task trials revealed that vividness ratings are less related to memory details in older than in young adults (Folville, D'Argembeau et al., 2020; Folville, Jeunehomme et al., 2020; Folville, Vandeleene et al., 2021). Relative to their younger counterparts, older adults may differentially attend to visual features during memory encoding (Mitchell & Hill, 2019; Mitchell & Johnson, 2009) and they might use/monitor these details differently during memory retrieval (Johnson et al., 2015; Koutstaal, 2003), which might explain why their subjective vividness ratings are less closely tied to memory details (Folville, D'Argembeau et al., 2020).

An age-related diminution in brain activity, as measured with univariate fMRI analyses, has been widely reported in episodic memory tasks both during encoding and retrieval (Craik & Rose, 2012; Dennis & Cabeza, 2015; Nyberg, 2017). Relative to their younger counterparts, older participants show less brain activity in the hippocampus, the fusiform gyrus and the parahippocampal cortex when remembering the source (Cansino et al., 2015) or details (Addis et al., 2011) from past events. Additionally, a few studies have revealed that the intensity of older adults' vividness ratings contrasted with the age-related reduction in brain activity observed in the fusiform gyrus and the precuneus, brain regions devoted to the visual processing and the mental imagery of memory features, respectively (Folville, Bahri et al., 2020; McDonough et al., 2014). Normal aging is further characterized by a deficient neuromodulation, which yields a decrease of the specificity, the stability and the distinctiveness of neural representations (Li et al., 2000, 2001). Also known as age-related *neural dedifferentiation*, this phenomenon reflects the lack of

selectivity – distinctiveness- of the neural responses associated with the processing of different types of items or stimulus categories (Abdulrahman et al., 2017; Deng et al., 2021; Koen & Rugg, 2019; Koen et al., 2020).

Particularly useful to study age-related differences in neural specificity are recent multivariate fMRI methods such as Pattern Similarity Analyses (PSA), by which the neural patterns of brain activity associated with the processing of one item can be examined across different occurrences (Dimsdale-Zucker & Ranganath, 2019; Kriegeskorte et al., 2008). While traditional univariate fMRI analyses measure the mean BOLD signal intensity in each voxel, multivariate methods such as PSA examine BOLD responses across groups of voxels (Chadwick et al., 2012). Examining the BOLD signal across groups of voxels, rather than in each voxel separately, offers the advantage of giving insights about *representations* of cognitive states or stimulus (Kriegeskorte et al., 2008; Norman et al., 2006). Another great advantage of multivariate PSA is that they allow an examination of patterns of brain activity at the trial level. In the context of episodic memory tasks, PSA analyses can be conducted by examining the correlation of neural patterns of brain activity across the repetition of one particular item (Trelle et al., 2019; Zheng et al., 2018). Using this analytical approach, previous evidence has revealed that older participants' neural representations were less similar than those of young adults across the repeated viewing of the same stimulus in the fusiform gyrus, parahippocampal regions and occipital cortex (Carp et al., 2011; Kobelt et al., 2021; M. St-Laurent et al., 2014; Trelle et al., 2019; Zheng et al., 2018). Healthy aging also reduces the specificity of neural representations during memory retrieval, with older participants having less specific neural representations in temporal regions than young adults (Marie St-Laurent et al., 2019; M. St-Laurent et al., 2014).

In summary, normal aging reduces the capacity to encode and recollect specific details from past events but older adults do not subjectively judge the quality of these memories as impoverished. Moreover, aging decreases the specificity of neural representations underlying the encoding and the retrieval of episodic memory traces in brain regions devoted to the visual and spatial processing of picture stimuli.

Over the past decades, episodic memory studies have focused on how information could be encoded, stored and retrieved within each individual's mind. Yet, memories often relate to events that have been experienced by a few persons (e.g., family members remembering a conversation; Hirst & Echterhoff, 2012), a community (e.g., fans of a football team remembering a match; Merck et al., 2020) or a nation (e.g., American citizens remembering the unfolding of the Vietnam war; Zaromb et al., 2014). This implies that individuals, who never met in some cases, may have memory representations that encompass similar event details. Particularly interesting to illustrate this phenomenon are behavioral studies showing that participants remember the same words (Verhaeghen & Marcoen, 1993), pictures (Bainbridge, 2020; Bylinskii et al., 2015; Isola et al., 2011) or event details (Cheriet et al., 2021; Merck et al., 2020; Zaromb et al., 2014) in episodic memory tasks. Since PSA measure patterns of neural activity at the trial level and allow the examination of stimuli representations within the brain, some authors have used these analytic procedures to investigate whether patterns of brain activity were similar between individuals processing the same stimulus or event. Notably, a precursor study showed that participants viewing the same portions of films shared similarities in the patterns of brain activations, not only in primary visual areas, but also in associative areas (Chen et al.,

2017; see also, Koch et al., 2020). Similar results have been put forward by Xiao and colleagues who showed that participants viewing the same pictures displayed across-participants neural similarity in occipito-temporal visual brain regions (Xiao et al., 2020). Given that episodic remembering involves the reactivation of brain patterns of activations from encoding (Rugg et al., 2015; Wheeler et al., 2000), Chen and colleagues recently examined whether participants remembering the same portions of films would show similarities in the patterns of cortical reactivation (Chen et al., 2017). Multivariate PSA yielded neural similarity in widespread posteromedial and occipito-temporal visual brain regions (Chen et al., 2017; see also, Xiao et al., 2020). Interestingly, a direct comparison of across-participants' value of neural similarity during memory encoding and retrieval revealed that neural similarity measured between participants was higher in ventral visuals areas during memory encoding compared with memory retrieval, while neural similarity was higher in angular gyrus and medial prefrontal cortex during memory retrieval relative to encoding (Xiao et al., 2020).

To date, age differences in across-participants' similarity of the neural patterns of brain activity have been scarcely studied in the literature. Previous evidence has shown an age-related decrease in inter-subject neural synchronization in frontal and temporal brain regions across older adults viewing the same video, thus suggesting that older individuals might display more idiosyncratic neural responses than young adults (Campbell et al., 2015; Geerligs & Campbell, 2018). Yet, these studies examined the similarity of brain processing across older participants by using inter-subjects correlations, rather than using multivariate analyses conducted at the trial level such as PSA. Besides, above-mentioned studies examined age-differences in inter-subjects brain synchronization during the viewing of videos only, so that it is currently unknown whether neural similarity measured across individuals is diminished in older participants remembering those stimuli. Examining whether the neural traces supporting the visual processing and the reinstatement of memory features are similar across young and older participants could notably shed new lights on age-related differences in the basis of subjective memory vividness. Indeed, if older adults do rely less than young adults on visual episodic details to frame their subjective sense of memory vividness (Folville, D'Argembeau et al., 2020; Folville, Vandeleene et al., 2021), then neural similarity should be reduced across older participants who make strong vividness ratings for the same memory events. Besides, examining whether aging reduces the specificity of neural representations when it is examined across, rather than within, participants could provide new insights about age-related differences in the differentiation of neural traces supporting memory encoding and retrieval processes. In the present article, we report a multivariate PSA of Folville et al.'s (2020) data-set to assess the similarity of neural patterns of activation across participants. More specifically, we examined the specificity of the neural representations underlying the encoding and the remembering of vivid memories. Based on previous above-mentioned work, we should observe across-participants' neural similarity in occipital-temporal and visual areas during memory encoding in young adults, while neural similarity should be diminished in the older age-group in these regions. During vivid memory retrieval, across-participants' neural similarity should be higher in young than in older participants in parietal brain regions supporting the reinstatement of event memory details.

Methods

Data presented below have already been used in one previous publication (Folville, Bahri et al., 2020) but the analyses and results reported in the present paper are new and have not been reported in any previous work/publication. Data reported in the present paper can be obtained upon request.

Participants

Twenty-two young (14 women; M_{age} = 23.73; SD_{age} = 1.88) and 21 older (9 women; M_{age} = 70.19; SD_{age} = 6.23) participants were included in the analyses reported here. Participants had normal or corrected-to-normal vision. Older participants were screened with the Dementia Rating Scale (Mattis, 1976) and all performed within the norms (Pedraza et al., 2010). Age-groups did not differ in terms of education or mental imagery capacity (measured with the VVIQ; Marks, 1973). The experiment was approved by the ethic committee of the Medical Faculty of the University of Liège. More information regarding the description of the sample can be found in Folville et al. (2020).

Material

Stimuli were 80 colored pictures depicting scenes selected from the NAPS (Marchewka et al., 2014). All selected pictures were neutral and their valence ranged from 4.25 to 6.88 (M = 5.45; SD = 0.60). Like in a previous study (McDonough et al., 2014), each picture was associated with a verbal label from 1 to 3 words. Pictures were split in four sets of 20 pictures each. Three sets were used as targets while the remaining set was used for a lure condition (not analyzed here).

Procedure

Both the encoding and the retrieval phase were scanned (these sessions are represented on Figure 1). During encoding, participants were presented with the verbal label for 1500 milliseconds (ms), followed by the presentation of the corresponding picture for 7000 ms (n = 60 trials; Figure 1(a)). For some trials (n = 20), the presentation of the label was not followed by any picture (i.e., lure condition). Trials were presented in a predefined random order. Each encoding trial was separated by a fixation cross of variable duration (jitter: 1000 to 2000 ms). Participants were aware that they should memorize both the picture and its corresponding label in preparation for the subsequent cued-recall phase. The encoding and the retrieval phase were separated by a structural MRI scan for 5 minutes.

Retrieval took the form of a cued-recall task in which participants were presented with the verbal labels only. Label presentation had a duration of 5000 ms during which participants were instructed to remember the associated pictures in as much details as possible (Figure 1(b)). Next, participants rated the vividness of their memory using a scale ranging from 0 to 3. Participants were given a maximum of 5000 ms to make their ratings and the scale disappeared once a response was made. Participants were instructed that they should answer 0 if they could not recollect the picture while ratings

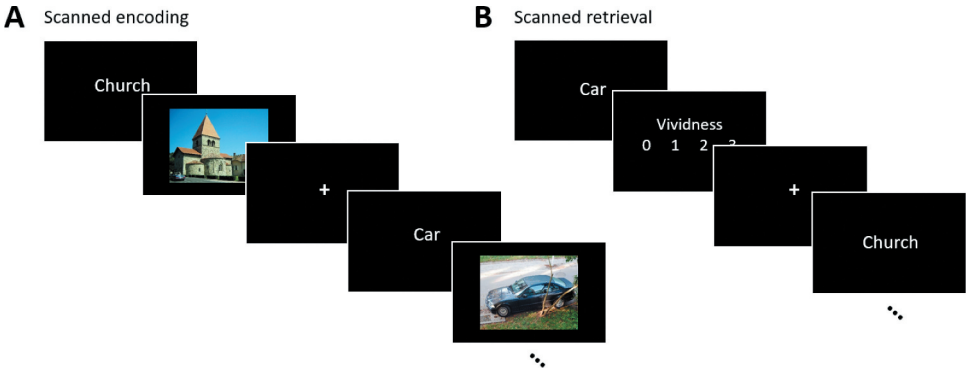

Figure 1. (a). Memory encoding task with two representative trials during which participants first viewed a descriptive label followed by the corresponding picture. (b). Memory retrieval task in which participants were presented with the label from which they were instructed to remember the associated picture before making a vividness rating (0, 1, 2 or 3) .

of 1, 2 and 3 corresponded to low, medium and high vividness intensity, respectively. A fixation cross of variable duration was presented between each retrieval trial (jitter: 2000 to 5000 ms). After the scanning session, participants took part to a behavioral cued-recall phase. Description and results of this task can be found in Folville et al. (2020).

MRI acquisition

Images were acquired using a 3 T Siemens Scanner (Magnetom Prisma). T2-weighted Echo-Planar imaging (EPI) was used (36 slices, TR = 2246 ms, TE = 30 ms, FA 90°, FOV 192 × 190 mm^2, voxel size 3 x 3 x 3.75 mm^3, interleaved slice ordering) for encoding and retrieval sessions. Around 303 and 330 functional volumes were acquired respectively at the encoding and retrieval sessions. The first 3 volumes of each session were discarded to account for T1 saturation. A structural MR scan was acquired between the two EPI sessions with the following parameters: T1-weighted 3D magnetization-prepared rapid acquisition gradient echo (MP-Rage), TR = 1960 ms, TE = 4.43 ms, FOV = 230 x 173 mm^2, voxel size 0.9 × 0.9 x 0.9mm^3. After the two EPI acquisitions, field maps were acquired using two gradient-recalled sequences (TR = 367 ms, TE = 4.92 & 7.38, FA 90°, FOV 230 × 230 mm^2).

fMRI preprocessing

Data preprocessing was carried out using Statistical Parametric Mapping software (SPM 12; Wellcome Trust Center for Neuroimaging, London, United-Kingdom). For each participant, both EPI time-series sessions were reoriented into the MNI space using the SPM template, then corrected for motion and distortion (using 6 nuisance regressors) using Realign and Unwarp (Andersson et al., 2001) together with the FieldMap toolbox (Hutton et al., 2002), and coregistered to the corresponding structural image. The structural image was then segmented into gray and white matter using unified

segmentation (Ashburner & Friston, 2005). The warping parameters were then separately applied to the functional and structural images to produce normalized images with isotropic voxel size of 2 and 1 mm, respectively. Like in previous studies using multivariate PSA analyses (Hill et al., 2021; Wing et al., 2015), functional images were left unsmoothed.

Across-participants Pattern Similarity Analyses (PSA)

Pattern Similarity Analyses (PSA) were used to examine neural similarity across-participants. Analyses were restricted to encoding and retrieval trials of pictures that received of a vividness rating of 3 during retrieval (Mean number of trials in young participants = 31.18 (SD = 10.85); Mean number of trials in older participants = 41.95 (SD = 12.66); $t(41) = 2.99$, $p = .005$).[1] We used a general linear model with separate regressors for each task trial (although the analysis focused on high vividness trials, all trials were included in the model, see, Rissman et al., 2004). Each task trial was modeled as a 0-second duration event. Were also included in the model regressors corresponding to realignment and nuisance parameters to model movement-related variance. The CoSMoMVPA toolbox (Oosterhof et al., 2016) was then used to perform PSA using the resulting betas. To examine neural similarity across-participants, a searchlight procedure was used (Kriegeskorte et al., 2008), with $3 \times 3 \times 3$ voxel cubes.

Two types of analyses were used. First, the encoding x encoding analysis examined across-participants' neural similarity during memory encoding. The analysis procedure was inspired from the one used by Chen and colleagues (2016). For each participant, the neural pattern of each encoding trial (e.g., the picture depicting a church) was correlated with the neural pattern of that trial (i.e., the church) averaged across the remaining participants (i.e., item-level; see, Figure 2(a)). Across-participants' neural similarity during encoding was also measured at the set-level, in which the neural patterns of one encoding trial were correlated with the neural patterns of each of the remaining encoding trials (i.e., the other scenes: church x keyboard, church x car . . .) averaged across the remaining participants (Figure 2(a)). These correlations were then averaged to obtain one set value per trial and per voxel. The set-level was used as a baseline level as it reflects the neural similarity of low-level visual processes that are not item-specific (Ritchey et al., 2013).

Second, the retrieval x retrieval analysis examined across-participants' neural similarity during memory retrieval. This analysis was conducted exactly in the same way as the encoding x encoding analysis, with across-participants neural similarity being investigated both at the item and set-levels for stimuli from the retrieval phase.

In previous studies examining across-participants' neural similarity in young individuals, neural patterns of brain activity of one participant were correlated with the corresponding neural patterns of the remaining participants of his/her group (Chen et al., 2017). As the present experiment included both young and older participants, each type of across-participants' similarity analysis (encoding x encoding and retrieval x retrieval) was conducted using two procedures. In the first one, similarity analyses were conducted **within** one participant's age-group (Figure 2(b)). In other words, neural traces of one young participant were correlated with the corresponding neural traces averaged across the remaining young participants (young within-group) and the same was true for older participants (older within-group). In the second analysis, neural patterns were

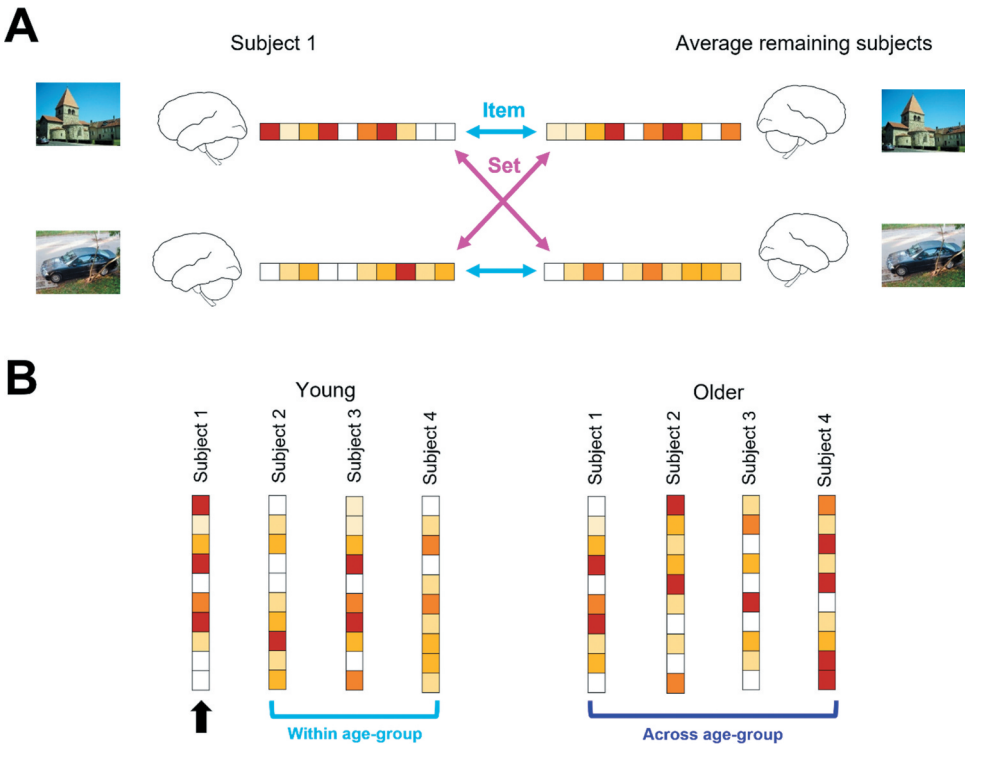

Figure 2. Visual representation of the Pattern Similarity Analyses (PSA). (a). For the item-level, neural patterns of each picture for one participant were compared with the neural patterns of the corresponding picture averaged across the remaining participants. For the set-level, neural patterns of each picture for one participant were compared with the neural patterns of the remaining pictures. (b). Each participant (e.g., subject 1 of the young age-group) was either compared with the remaining participants of his/her age-group (within age-group) or with the participants of the other age-group (across age-group) .

analyzed **across** age-groups. In other words, neural traces of one participant of one age-group were correlated with the corresponding neural traces averaged among the participants of the other age-group. For instance, neural patterns of the first young participant were correlated with the averaged patterns of the older participants (i.e., young across-group; Figure 2(b)) and vice-versa (i.e., older across-group; Figure 2(b)). With such analysis, one older participant having youth-like neural representations of the pictures would potentially have as high across-participants similarity values as young participants, thus perhaps revealing the heterogeneity of the specificity of neural representations among the sample of older participants.

Statistical analyses

Pearson correlations resulting from the searchlight procedure were Fisher-transformed for statistical analyses. These statistical analyses were conducted using SPM 12. To examine age-differences in across-participants' neural similarity, we performed 2 (Age-groups:

young vs. older) x 2 (Levels: item vs. set) factorial ANOVAs on across-participants' similarity maps for encoding and retrieval sessions. These analyses were first conducted using across-participants' similarity maps that were specific to each age-group separately (young within-group and older within-group). To examine whether age-differences in across-participants' neural similarity are impacted by the type of procedure used (i.e., within vs. across age-group), we performed 2 (Age-groups: young vs. older) x 2 (Procedure: within vs. across) factorial ANOVAs on item-level similarity maps for both encoding and retrieval sessions. Results of the ANOVAs were first examined using the F-statistics and the interactions were then explored using the t-statistics. We indeed hypothesized a priori that item values should be higher than set values in young but not in older participants. Consistently with previous PSA studies (Bird et al., 2015; Oedekoven et al., 2017), a cluster-defining threshold of $p < .001$ with clusters significant at $p < .05$ (FWE cluster corrected) was used.

We further examined whether older participants displayed any significant across-participants similarity values during memory encoding and retrieval. To do so, we compared older participants' item similarity values against zero using a one-sample t-test for each session.

Because we expected neural similarity to be reduced in the older age-group, we also investigated whether running the across-participants neural similarity analysis with the same group as brain average (e.g., the average of young adults) would narrow age-differences in neural similarity. To examine this question, we conducted a two-sample t-test between item similarity values of young adults compared within their own group (i.e., young within) and older adults compared with the average of the young group (i.e., older across). The same analysis with the older age-group as brain average was also conducted (i.e., item-level young across minus item-level older within). The same statistical threshold as in the ANOVAs was used for the t-tests.

Results

Encoding x encoding, within age-group

We first examined age-differences in across-participants' neural similarity during memory encoding with similarity values computed within each age-group separately. The Age-groups x Levels factorial ANOVA on across-participants' similarity values computed within each age-group yielded a significant Age-groups x Levels interaction with the contrast [(young-item)-(young-set)>(older-item)-(older-set)] in a large bilateral cluster encompassing the middle/superior occipital gyrus and the cuneus (Table 1 and Figure 3). This interaction showed that item values were higher than set values in young adults but not in older adults (Figure 3). The interaction could be also observed in clusters located in posterior parietal and superior and middle frontal areas (Table 1).

We next examined whether older participants, despite showing a reduced difference between item and set levels in the previous analysis, would show significant (i.e., higher than zero) item similarity values. Using a one-sample t-test, we found that older participants showed significant item similarity values in several brain regions including, but not limited to, bilateral occipital areas (calcarine cortex), the left temporal pole, the left

Table 1. Coordinates of the across-participants' neural similarity comparisons during memory encoding.

Region	Hemisphere	MNI coordinates			t-value	k
		x	y	z		
Encoding x encoding, within age-group						
Age-groups x Levels interaction						
Precuneus/Inferior and middle occipital gyrus	L/R	−18	55	20	7.65	2093
Frontal operculum	L	−42	11	17	7.52	83
Cerebellum	L	−18	−49	−52	6.18	108
Anterior cingulate gyrus/medial frontal cortex	L/R	−3	38	11	6.97	636
Cerebellum	R	3	−82	−31	6.81	84
Occipital pole	R	18	−100	−1	6.23	344
Middle temporal gyrus	L	−63	−37	−7	6.12	43
Superior parietal lobule/postcentral gyrus	R	30	−40	59	6.06	262
Lateral orbital gyrus	L	−33	38	−4	5.35	38
Caudate	L	−12	5	2	5.31	32
Central operculum/postcentral gyrus	R	54	−13	20	5.26	27
Superior parietal lobule	L	−30	−43	59	5.24	77
Supramarginal gyrus	L	−51	−43	35	4.91	41
Inferior temporal gyrus/fusiform gyrus	R	51	−28	−19	4.91	45
Superior frontal gyrus	L	−15	5	53	4.90	63
Middle frontal gyrus	R	33	38	38	4.89	50
Cerebellum	R	33	−70	−31	4.82	30
Superior frontal gyrus	R	18	26	47	4.64	55
Encoding x encoding, within vs. across age-group						
Age-groups x Procedures interaction						
Occipital pole/Superior occipital gyrus/calcarine cortex	L/R	15	−97	−1	12.18	6977
Cerebellum	L	−3	−73	−43	6.08	45
Cerebellum	L	−18	−52	−52	5.72	44
Superior frontal gyrus	L	−3	38	35	4.63	30
Angular gyrus	L	−57	−58	38	4.56	27
Superior frontal gyrus	R	6	53	−7	4.47	26
Middle frontal gyrus	L	−30	32	35	4.40	33

superior and medial frontal cortex. These brain regions are depicted in Figure 4 (below left), along with the results obtained from the same analysis conducted in young adults for visual comparison (Figure 4 top left).

Encoding x encoding, within versus across age-group

Next, we examined whether item-level similarity values during encoding would be impacted by the type of procedure used (i.e., neural similarity computed within or across age-group). The 2 Age-groups (young vs. older) x 2 Procedures (within vs. across) factorial ANOVA on item-level similarity values yielded a significant Age-groups x Procedures interaction with the contrast [(young within)-(young across)>(older within)-(older across)] in widespread clusters in occipito-temporal brain regions (i.e., bilateral occipital gyrus, lingual gyrus, calcarine cortex and fusiform gyrus, see, Table 1). This pattern of findings suggests that item-level similarity values were higher in young than in older adults when similarity was measured within each participant's age-group while item-level similarity values were higher in older than in young adults when neural similarity was examined across each participant's age-group (Figures 4 and 5).

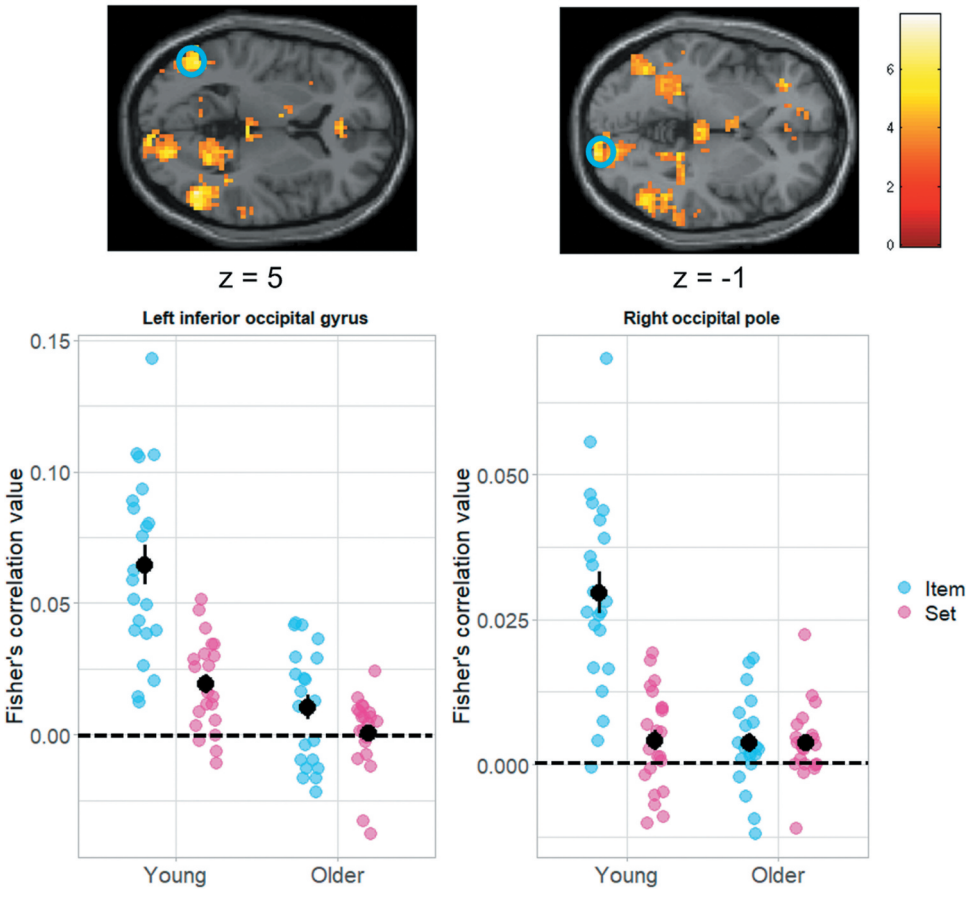

Figure 3. Plot of the across-participants' neural similarity values (i.e., Fisher's correlation values) for the item and the set-levels in the encoding x encoding analysis conducted within each age-group. Age-groups x Levels interaction in the left inferior occipital gyrus and the right occipital pole. Each circle represents an individual's participant data. These values were extracted from a sphere of a diameter of 3 mm that was centered on the local maxima of the cluster. Black circles and error bars represent the mean ± 1 standard-error of the mean (SEM).

To further examine whether comparing each older participant with the average of the young age-group would narrow age-differences in neural similarity, we conducted a two-sample t-test between item similarity values of young adults compared within their own group (i.e., young within) and older adults compared with the average of the young group (i.e., older across). Results revealed that older adults still had lower similarity values than young adults in the bilateral lingual and fusiform gyri. Similar results were obtained when taking the older age-group as brain average for both age-groups. A two-sample t-test between item similarity values of young adults compared with the average of the old group (i.e., young across) and older adults compared with the average of their age-group (i.e., older within) revealed that older adults had lower similarity values than young adults in the bilateral lingual gyrus and the left calcarine cortex.

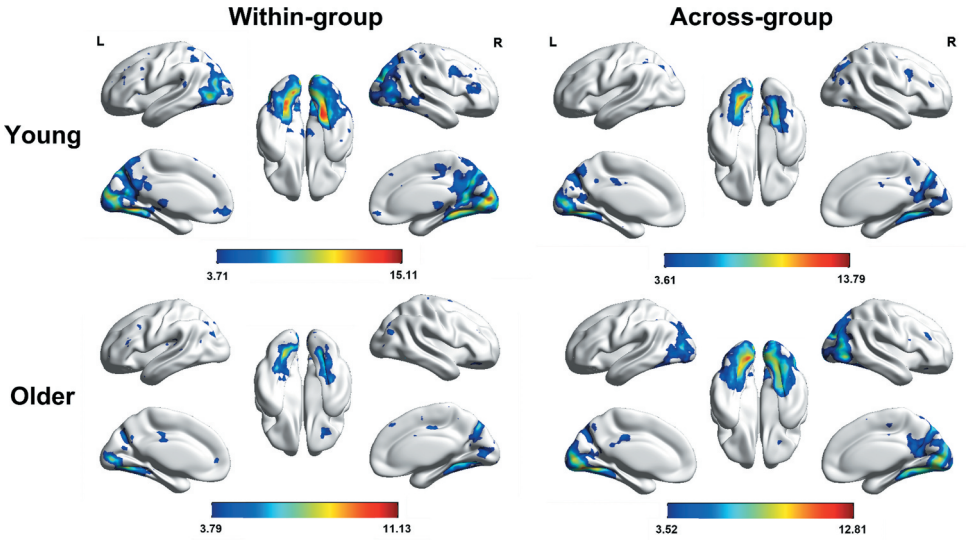

Figure 4. Within and across-group item-level neural similarity during memory encoding in young and in older participants. One-sample t-tests against zero were used in each age-group. Colors are in t-statistics units.

Retrieval x retrieval, within age-group

To assess age differences in neural similarity during memory retrieval, we conducted a 2 Age-groups (young vs. older) x 2 Levels (item vs. set) factorial ANOVA on across-participants' retrieval x retrieval similarity values computed within each age-group. It yielded a significant Age-groups x Levels interaction with the contrast [(young-item) -(young- set)>(old-item)-(old-set)] in bilateral clusters comprising the calcarine cortex, the lingual gyrus and the cuneus and in posterior parietal areas including the left angular gyrus and the left precuneus (Table 2 and Figure 6). This interaction showed that item values were higher than set values in young adults but not in older adults.

We next examined whether older participants would show significant (i.e., higher than zero) item similarity values. Results revealed that older participants showed significant item similarity values in the right superior and middle frontal gyrus, the left postcentral gyrus, the right temporal pole and the left calcarine cortex. These brain regions are depicted in Figure 7 (below left), along with the results obtained from the same analysis conducted in young adults for visual comparison (Figure 7 top left).

Retrieval x retrieval, within versus across age-group

Finally, we aimed at examining whether similarity values during memory retrieval would be affected by the type of procedure used (i.e., neural similarity computed within or across each participant's age-group). The 2 Age-groups (young vs. older) x 2 Procedures (within vs. across) factorial ANOVA on across-participants' similarity values yielded a significant Age-groups x Procedures interaction in several brain regions including the left lingual gyrus, the right occipital pole, the bilateral fusiform gyrus and the left

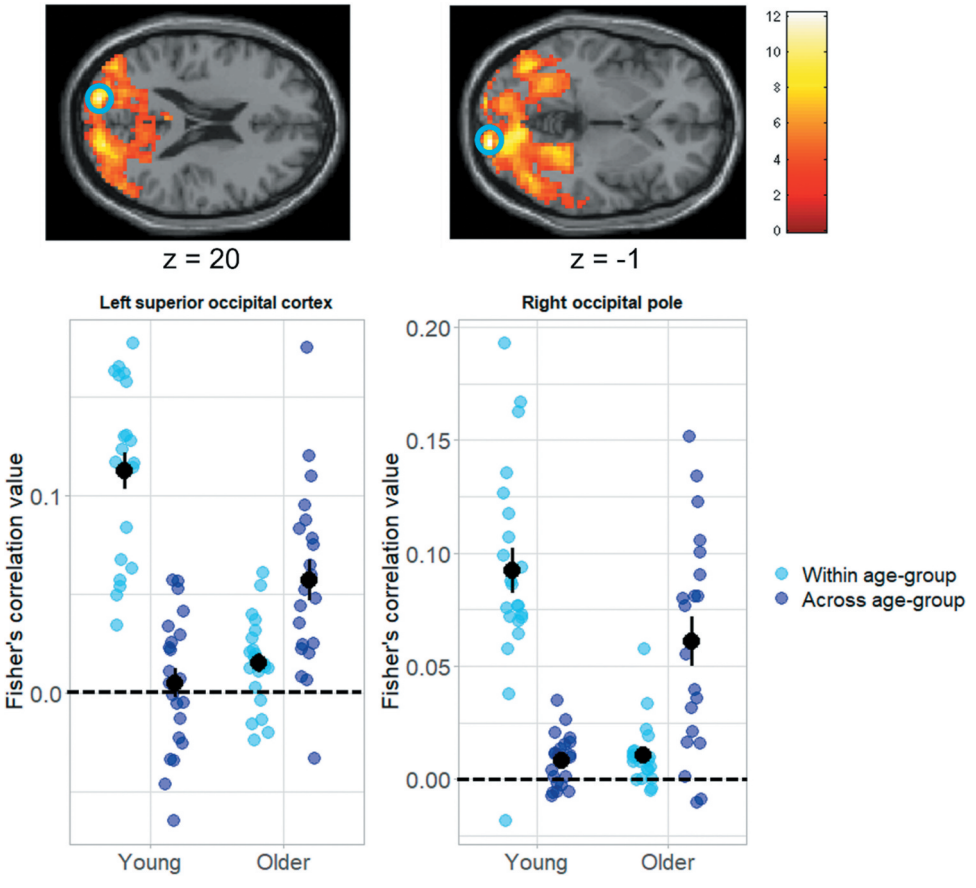

Figure 5. Plot of the across-participants' neural similarity values (i.e., Fisher's correlation values) for the item-level during memory encoding conducted either within or across each age-group. Age-groups x Procedures interaction in the left superior occipital cortex and the right occipital pole. Each circle represents an individual's participant data. These values were extracted from a sphere of a diameter of 3 mm that was centered on the local maxima of the cluster. Black circles and error bars represent the mean ± 1 SEM.

middle frontal gyrus (Table 2). This interaction showed that item-level similarity values were higher in young than in older adults when similarity was measured within each participant's age-group while item-level similarity values were higher in older than in young adults when neural similarity was examined using the other age-group pattern (Figures 7 and 8). We next examined whether comparing each participant with the average of the young age-group would attenuate age-differences in neural similarity by conducting a two-sample t-test between item similarity values of young (i.e., young within) and older adults (i.e., older across). Results revealed that older adults still had lower similarity values than young adults in brain regions comprising the right occipital pole/superior occipital cortex, the left inferior/middle temporal gyrus and the right parietal lobule. Again, comparing both young and older adults with the brain average of the old group yielded lower similarity values in older than in young adults. A two-

Table 2. Coordinates of the across-participants' neural similarity comparisons during memory retrieval.

Region	Hemisphere	MNI coordinates			t-value	k
		x	y	z		
Retrieval x retrieval, within age-group						
Age-groups x Levels interaction						
Angular gyrus/superior middle temporal gyrus	L	−53	−55	20	6.34	216
Posterior and middle orbital gyrus	L	−18	35	−16	6.26	60
Calcarine cortex/lingual gyrus/occipital pole	L	−3	−94	−4	4.74	70
Lingual gyrus	R	6	−67	−4	4.72	34
Retrieval x retrieval, within vs. across age-group						
Age-groups x Procedures interaction						
Lingual gyrus/calcarine cortex	L	−6	−94	−10	7.79	232
Occipital pole/calcarine cortex	R	18	−100	8	5.79	147
Inferior occipital gyrus/fusiform gyrus	L	−48	−70	−1	5.73	244
Supramarginal gyrus	R	45	−43	29	5.21	44
Middle frontal gyrus/precentral gyrus	L	−36	5	62	4.95	58
Middle frontal gyrus	R	39	38	20	4.95	46
Medial/anterior orbital frontal gyrus	L	−15	35	−16	4.91	26
Fusiform gyrus/parahippocampal gyrus	R	39	−40	−16	4.86	63

sample t-test between item similarity values of young adults compared with the average of the old group (i.e., young across) and older adults compared with the average of their age-group (i.e., older within) indeed revealed that older adults had lower similarity values than young adults in the left precuneus/postcentral gyrus, the left middle temporal/occipital gyrus and the right opercular part of the inferior frontal gyrus.

Discussion

We examined age differences in across-participants' neural similarity during memory encoding and retrieval. These analyses were conducted on high vividness trials only,[2] so that neural representations during memory encoding and retrieval were compared across participants experiencing a strong and intense subjective sense of recollection. Neural similarity was measured across participants while using two different procedures. In the first one, neural patterns were compared across participants within their age-group. These analyses revealed that, both during memory encoding and retrieval, patterns of neural activation were more similar across young participants remembering the same (i.e., item-level) than different pictures (i.e., set-level) in distributed occipital, temporal and parietal brain regions than across older adults. In the second procedure, patterns of brain activity were compared across age-groups so that each young participant was compared with the average of older adults and vice-versa. In young participants, running the similarity analysis across the older age-group dramatically reduced across-participants neural similarity values both during memory encoding and retrieval. The opposite pattern was found in older adults, with similarity values being higher in older participants when they were compared across young participants than within their own age-group.

Concerning memory encoding, we found that neural patterns were similar across young participants visualizing the same pictures while the correlations between the patterns associated with the visual processing of different pictures were lower. This finding is consistent with prior reports revealing similarity of brain patterns of neural

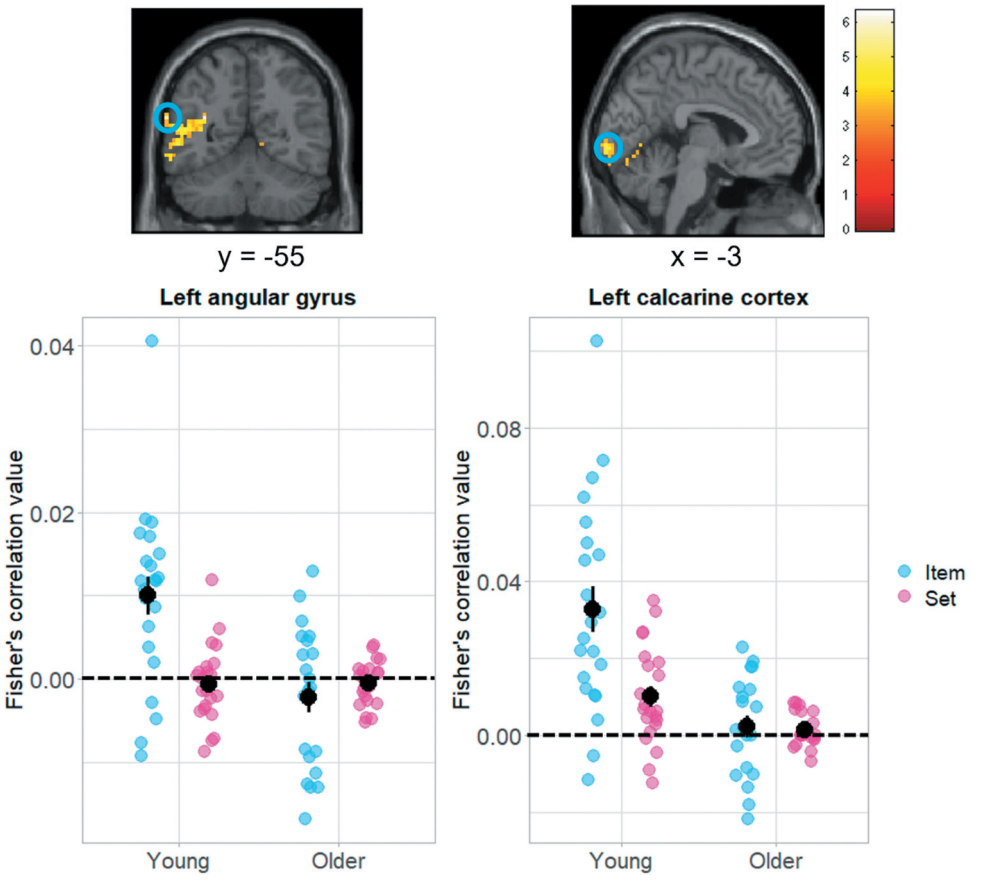

Figure 6. Plot of the across-participants' neural similarity values (i.e., Fisher's correlation values) for the item and the set-levels during memory retrieval conducted within or across each age-group. Age-groups x Levels interaction in left angular gyrus and the left calcarine cortex. Each circle represents an individual's participant data. These values were extracted from a sphere of a diameter of 3 mm that was centered on the local maxima of the cluster. Black circles and error bars represent the mean ± 1 SEM.

activations across young participants viewing the same portion of a film (Chen et al., 2017; Hasson et al., 2004), video clips (Koch et al., 2020), or discrete pictures (Xiao et al., 2020). Particularly interesting is that across-participants' similarity during encoding was observed in a large cluster extending over bilateral occipital and temporal brain regions (e.g., occipital cortex, temporal cortex, fusiform gyrus), which are associated with the processing of complex visual representations. These brain regions have been shown to be involved in the visual processing of scenes (Choi & Henderson, 2015; McDonough et al., 2014) and their components (e.g., buildings; see, Aguirre et al., 1998; Hasson et al., 2004). Across-participants neural similarity during viewing thus reveals similarity in how scenes' visual features were processed between participants. Neural similarity was however reduced, yet significant, in these regions when it was measured across older adults. This finding of an age-related reduction in across participants neural similarity echoes previous evidence showing reduced inter-subjects synchronicity of the time course of the brain

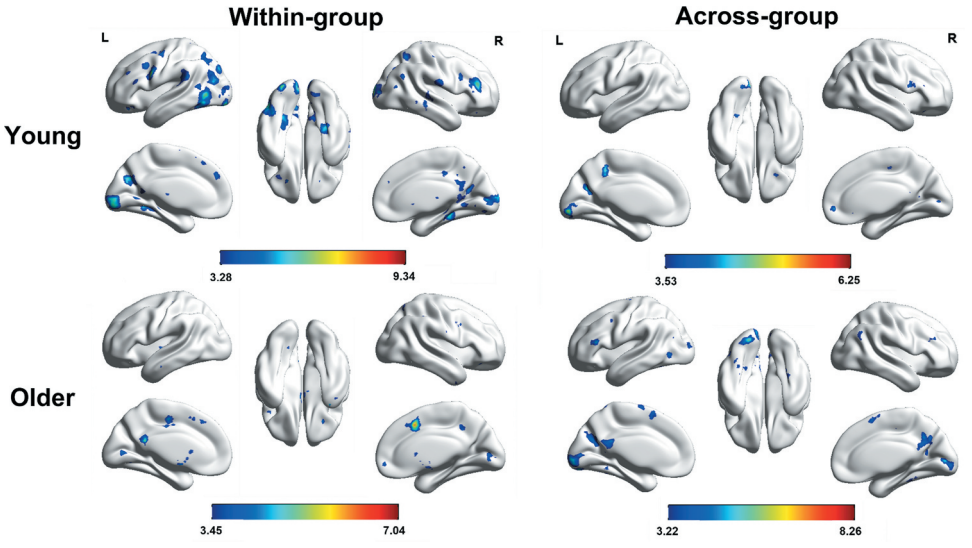

Figure 7. Within and across-group item-level neural similarity during memory retrieval in young (a) and in older participants (b). One-sample t-tests against zero were used in each age-group. Colors are in t-statistics units.

signal in older individuals (Campbell et al., 2015; Geerligs & Campbell, 2018). One hypothesis to explain the reduced neural similarity across older participants viewing the same scenes could be that older adults paid less attention to the "external" content of the pictures than young adults during encoding. Instead, older participants would have rehearsed "internal" information such as semantic autobiographical knowledge or personal memories related to the scenes (Mitchell & Johnson, 2009). It could also be that older adults had more attentional laps or engaged top-down attentional mechanisms to a lesser extent than young adults when viewing the stimuli (Campbell et al., 2015; Geerligs & Campbell, 2018). The reduced across-participants neural similarity in occipito-temporal visual regions could thus be attributed to older adults' tendency to focus their visual attention to a reduced extent on the content of pictures during memory encoding.

Turning to memory retrieval, across-participants' neural similarity was higher in young than in older participants in occipito-temporal areas (i.e., lingual gyrus/calcarine cortex) and parietal regions (i.e., angular gyrus and supramarginal gyrus). These findings echoes previous findings showing across-participants neural similarity in the angular gyrus and the ventral visual cortex during memory retrieval (Xiao et al., 2020). Previous evidence has revealed that the lingual gyrus was involved in the visual processing of scenes during memory encoding and retrieval (Machielsen et al., 1999). Finding across-participants' neural similarity in the lingual gyrus might thus reflect the reactivation of visual memory features in a comparable way across young participants. Within the posterior medial episodic network, angular gyrus has been identified as a key neural structure for the remembering of complex memory representations (Ritchey & Cooper, 2020). Angular gyrus notably supports the integration of multimodal event details (Tibon et al., 2019; Yazar et al., 2017; see, Humphreys et al., 2020 for a review). Consequently, the similarity of patterns of neural activity in these regions across young participants during memory

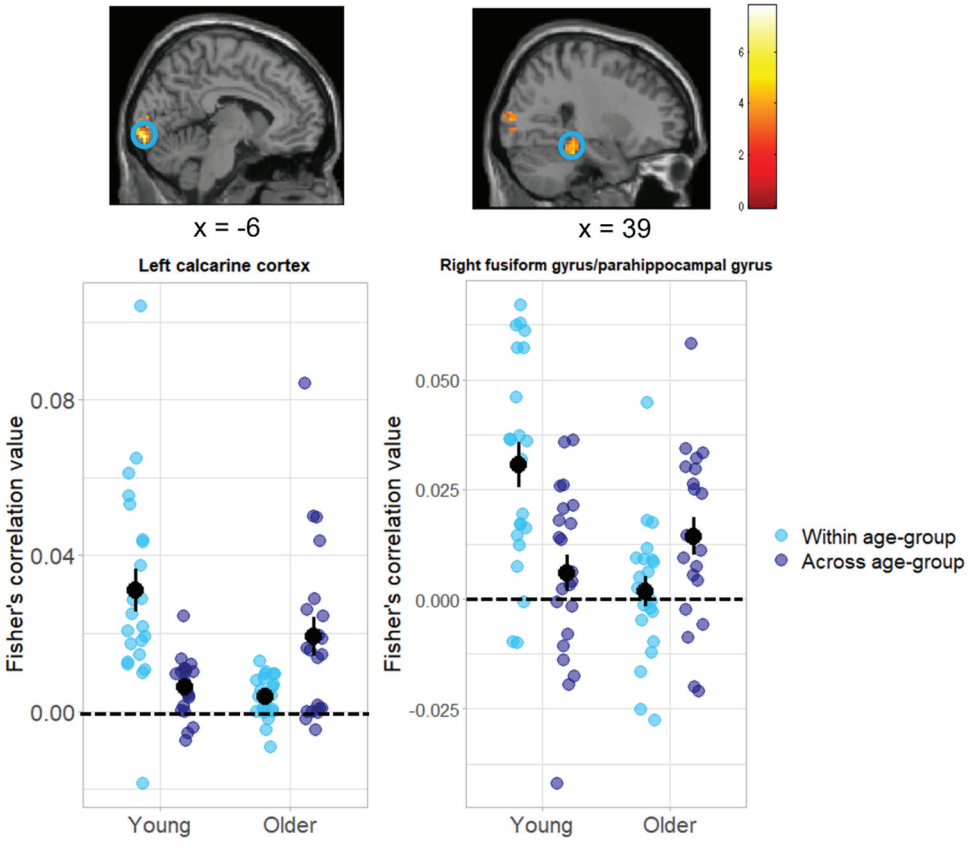

Figure 8. Plot of the across-participants' neural similarity values (i.e., Fisher's correlation values) for the item-level during memory retrieval conducted either within or across each age-group. Age-groups x Procedures interaction in left calcarine cortex and the right fusiform/parahippocampal gyrus. Each circle represents an individual's participant data. These values were extracted from a sphere of a diameter of 3 mm that was centered on the local maxima of the cluster. Black circles and error bars represent the mean ± 1 SEM.

retrieval might reflect the reactivation of comparable complex and rich memory representations of the scenes across participants remembering them. The present multivariate analyses also provide evidence that neural representations in parietal and occipito-temporal brain regions are less similar across older participants remembering the same pictures, thus suggesting that older participants remembering the same images might mentally visualize the features of the scenes in a way that greatly varies from one participant to another.

In the present study, we examined age-differences in across-participants neural similarity in the context of vivid recollection because we believed that the present analyses could shed new lights on age-related differences in memory vividness. During memory encoding, an age-related reduction in across-participants neural similarity was observed in brain regions that support the visual processing of the scenes while judging these traces as very vivid during retrieval. Thus, older adults would focus to a lesser extent on visual information during memory encoding and then they would also use them less than young adults to

inform their vividness ratings at retrieval (Johnson et al., 2015; Mitchell & Johnson, 2009). Also in support to this account is the finding that across-participants neural similarity was reduced in brain regions supporting the retrieval of visual memory details in the older age-group during memory retrieval. This provides additional evidence that older adults seem to use retrieved visual memory details to a lesser extent than young adults when making high vividness ratings during memory retrieval, although the reasons for why it might be the case are still debated (Folville, D'Argembeau et al., 2020; Folville, Simons et al., in press).

In addition to the aforementioned behavioral hypotheses that aimed at explaining age-related differences in across-participants neural similarity, the present results can be also interpreted considering inter-participants neural variability. With increasing age, inter-individual differences in brain and cognition become larger (Lindenberger, 2014). Notably, some older adults still show high performance in memory tasks, sometimes even as high as young adults, while others perform more poorly (LaPLume et al., 2021; Lindenberger, 2014). These larger individual differences in aging can be also observed both at the structural and functional brain level, with some older adults showing "youth-like" brain structure or activity (Nyberg et al., 2012). If memory performance and the corresponding neural activity are more variable among older adults, then one may wonder whether it would decrease the similarity of neural brain activity when it is measured across older individuals. For instance, previous evidence has shown that the dynamic course of brain responses was more variable in aging, with older adults displaying lower brain synchronicity than young adults when processing the same stimulus (Campbell et al., 2015; Geerligs & Campbell, 2018). In the present study, higher variability in the specificity of the neural traces in older than in young adults might reduce the extent of across-participants correlation values in the older age-group, and then influence the outcome of age-groups comparisons. Consistent with this hypothesis were the results of the across-groups neural similarity comparisons. These analyses revealed that older adults' similarity values were higher when each older participant was compared with the mean neural similarity values of young (i.e., older across age-group comparison) than with the remaining older adults (older within age-group comparison). In contrast, comparing each young participant with the average of older adults' neural brain signature (i.e., young across age-group comparison) dramatically decreased young participants' similarity values. Comparing members of any of the age-groups with the brain average of the older group thus yielded reduced neural similarity values. The reduced across-participants neural similarity in the older age-group may thus be explained by the fact that the brain average of their neural signals correlated only to a minor extent with individuals' neural representations. It could be that neural representations strongly varied from one older participant to another, which would result in a blurry average of brain signatures among the old group and which would in turn reduce measures of across-participants neural similarity (regardless of whether the participant compared with the brain average is young or older). In contrast, neural representations might be more similar across young participants, then resulting in a clear and distinct average of the brain patterns, which would in turn yield high correlations values between young group's brain average and individual participants' neural signatures.

The results described here can be also interpreted with respect to the age-related neural dedifferentiation account. According to this proposal, the distinctiveness and the specificity of neural representations is diminished in older individuals (Koen & Rugg,

2019; Koen et al., 2020), perhaps because of an age-related deficiency in neuromodulation (Li et al., 2000, 2001). Neural dedifferentiation has also been extensively examined via the similarity of neural representations associated with the repeated processing of individual items. For instance, item-level neural similarity across the visualization of the same picture is diminished in older compared to young adults, with lower similarity values in occipito-temporal regions such as inferior occipital cortex, and posterior parts of the fusiform and lingual gyri (Kobelt et al., 2021; M. M. St-Laurent et al., 2014; Trelle et al., 2019). Here, an age-related reduction in neural similarity examined across participants was observed in the same occipital areas, which suggests that the age-related neural dedifferentiation may be evident in posterior visual regions both at the within and across-participants levels. This is consistent with recent data showing that sensory features of visual scenes (modeled by means of Deep Convolutional Neural Network) were less differentiated in older than in young adults in the cuneus and the lingual gyrus (Deng et al., 2021). An age-related neural dedifferentiation may also be apparent during memory retrieval, with less similar neural representations in parietal and occipito-temporal brain regions within (M. St-Laurent et al., 2014) or across participants (the present study).

Relevant to illustrate the age-related deficit in neural differentiation in the present study is the finding that older adults' neural similarity values were, on average, still lower than those of young adults when all participants were compared with the same brain average. In other words, even when each participant was compared with the same average of patterns of brain activity (e.g., the average of young adults' neural representations), young adults (i.e., young within comparison) still showed higher across-participants neural similarity values than older adults (i.e., older across comparison). If older participants had as specific neural representations as young adults, then conducting across-participants analyses with the same brain average for both age-groups (thus ruling out any age-group difference in the distinctiveness of the brain average), should have yielded comparable neural similarity values between young and older participants here. This was however not the case. We therefore assume that the age-related reduction in across-participants neural similarity observed in the present study could be attributed to: 1) more variable neural representations between older participants at the group level; 2) overall less differentiated/specific neural representations at the individual level.

Strikingly, some older participants did show as high across-participants similarity values as young adults in occipito-temporal visual and associative brain regions during encoding (Figure 5) and retrieval (Figure 8). This finding is interesting and echoes evidence examining pattern of neural activity within participants and showing that some older adults had as high values indexing neural differentiation as young adults (Hill et al., 2021; Koen et al., 2019). It is also in line with recent findings showing that older adults maintaining youthful cognitive abilities had neural traces that were as differentiated as those of young adults (Katsumi et al., 2021). Future studies should thus seek to determine the cognitive and environmental factors that may help older adults in maintaining specific and differentiated neural representations.

The results of the present study also rise other several important avenues for future research. For instance, future studies should examine age-differences in across-participants similarity at different representational levels. While the present study and others (M. St-Laurent et al., 2014; Trelle et al., 2019) have examined patterns of neural similarity by means of PSA conducted at the item level, some studies have examined neural similarity at the category level. In the context of PSA, category-level analyses are measured by correlating the neural patterns of activity of one item with one other item (or the average of the remaining items; Hill et al., 2021; Koen et al., 2019) belonging to the same category (Koen & Rugg, 2019). Here, across-participants' neural similarity was not measured at the category-level, mainly because we did not use different types of picture categories (e.g., scenes vs. faces), but future studies should investigate age-differences in neural similarity using that measure. Also of importance for future works will be the examination of the factors that might exert an influence on measures of neural similarity conducted across participants. Notably, aging is characterized by changes in the hemodynamic BOLD signal, thus raising concerns about the validity of age-groups comparisons of patterns of brain activation (Esposito et al., 2003; West et al., 2019). Although noise in the BOLD signal should impact measures of multivariate pattern similarity only to a minor extent (Dimsdale-Zucker & Ranganath, 2019), whether and how age-related changes in the dynamic of the BOLD signal affect the observed pattern of across-participants neural similarity in the older age-group remains unknown and should be investigated in future research. Another interesting question regarding the use of across-participants PSA would be to determine how the sample size impacts the outcome of the analyses, as each participant is compared with the mean neural signature of his/her group.

To sum up, the current study examined for the first time age-differences in neural similarity measured across-participants during memory encoding and retrieval. While we found item-specific neural similarity in brain regions responsible for the visual processing of scenes across young participants visualizing the same pictures, neural similarity was reduced in older adults. The same was true during memory retrieval, with young adults showing across-participants neural similarity in parietal and occipital brain areas when vividly remembering pictures while older participants exhibited a reduction in neural similarity. While young participants may attend to the same features during memory encoding, and presumably use these features to inform their vividness ratings at retrieval, we assume that older adults visualizing and remembering the same pictures may not attend to the same features, hence reducing the magnitude of across-participants' neural similarity relative to young adults. We also interpret these results as evidence that older adults may have less specific and more variable neural representations than young adults. Although the present research extends previous findings by providing the first evidence that aging reduces the similarity of neural representation measured across-participants, it also raises numerous questions that future works should address. Future studies should notably examine in more detail how aging affects across-participants' neural similarity at different representational levels (i.e., item vs. categorical) as well as whether it relates to behavioral performance or individual differences in cognitive functions (Kobelt et al., 2021; Koen & Rugg, 2019; Koen et al., 2020).

Notes

1. It was not possible to examine age-differences across different memory vividness levels in the present study because older adults mostly expressed their subjective vividness ratings by using the maximum level of the scale (i.e., ratings of 3) and therefore did not have enough trials in lower vividness levels.
2. Note that similar results as those reported here were obtained when examining across-participants neural similarity on hit trials (i.e., trials that received vividness ratings of 1, 2 or 3, see the supplementary material section).

Acknowledgments

The authors wish to thank Nikita Beliy for his help with the Matlab codes and two Reviewers whose comments were very helpful in improving the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the Fund for Scientific Research (FRS-FNRS) under grant number (F 06/40/05 – FRESH/FC) attributed to AF. ED and CB are respectively Postdoctoral Researcher and Senior Research Associate at the FRS-FNRS.

ORCID

Emma Delhaye http://orcid.org/0000-0001-9224-267X

References

Abdulrahman, H., Fletcher, P. C., Bullmore, E., & Morcom, A. M. (2017). Dopamine and memory dedifferentiation in aging. *NeuroImage*, *153*(3), 211–220. https://doi.org/10.1016/j.neuroimage.2015.03.031

Abram, M., Picard, L., Navarro, B., & Piolino, P. (2014). Mechanisms of remembering the past and imagining the future - New data from autobiographical memory tasks in a lifespan approach. *Consciousness and Cognition*, *29*(1), 76–89. https://doi.org/10.1016/j.concog.2014.07.011

Addis, D. R., Musicaro, R., Pan, L., & Schacter, D. (2010). Episodic simulation of past and future events in older adults: Evidence from an experimental recombination task. *Psychology and Aging*, *25*(2), 369–376. https://doi.org/10.1037/a0017280.Episodic

Addis, D. R., Roberts, R. P., & Schacter, D. L. (2011). Age-related neural changes in autobiographical rememberingand imagining. *Neuropsychologia*, *49*(13), 3656–3669. https://doi.org/10.1016/j.neuropsychologia.2011.09.021.Age-related

Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). An area within human ventral cortex sensitive to "building" stimuli: Evidence and implications. *Neuron*, *21*(2), 373–383. https://doi.org/10.1016/S0896-6273(00)80546-2

Andersson J LR, Hutton C, Ashburner J, Turner R and Friston K. (2001). Modeling Geometric Deformations in EPI Time Series. NeuroImage, 13(5), 903–919. 10.1006/nimg.2001.0746

Ashburner J and Friston K J. (2005). Unified segmentation. NeuroImage, 26(3), 839–851. 10.1016/j.neuroimage.2005.02.018

Bainbridge, W. A. (2020). The resiliency of image memorability: A predictor of memory separate from attention and priming. *Neuropsychologia*, *141*(January), 107408. https://doi.org/10.1016/j.neuropsychologia.2020.107408

Bayen, U. J., & Murnane, K. (1996). Aging and the use of perceptual and temporal information in source memory tasks. *Psychology and Aging*, *11*(2), 293–303. https://doi.org/10.1037/0882-7974.11.2.293

Bird, C. M., Keidel, J. L., Ing, X. L. P., Horner, X. A. J., & Burgess, N. (2015). Consolidation of Complex Events via Reinstatement in Posterior Cingulate Cortex. *Journal of Neuroscience*, *35*(43), 14426–14434. https://doi.org/10.1523/JNEUROSCI.1774-15.2015

Bylinskii, Z., Isola, P., Bainbridge, C., Torralba, A., & Oliva, A. (2015). Intrinsic and extrinsic effects on image memorability. *Vision Research*, *116*(11), 165–178. https://doi.org/10.1016/j.visres.2015.03.005

Campbell, K. L., Shafto, M. A., Wright, P., Tsvetanov, K. A., Geerligs, L., Cusack, R., Tyler, L. K., Brayne, C., Bullmore, E., Calder, A., Dalgleish, T., Duncan, J., Henson, R., Matthews, F., Marslen-Wilson, W., Rowe, J., Cheung, T., Davis, S., Kievit, R., & Villis, L. (2015). Idiosyncratic responding during movie-watching predicted by age differences in attentional control. *Neurobiology of Aging*, *36*(11), 3045–3055. https://doi.org/10.1016/j.neurobiolaging.2015.07.028

Cansino, S. (2009). Episodic memory decay along the adult lifespan: A review of behavioral and neurophysiological evidence. *International Journal of Psychophysiology*, *71*(1), 64–69. https://doi.org/10.1016/j.ijpsycho.2008.07.005

Cansino, S., Trejo-Morales, P., Estrada-Manilla, C., Pasaye-Alcaraz, E. H., Aguilar-Castañeda, E., Salgado-Lujambio, P., & Sosa-Ortiz, A. L. (2015). Brain activity during source memory retrieval in young, middle-aged and old adults. *Brain Research*, *1618*(8), 168–180. https://doi.org/10.1016/j.brainres.2015.05.032

Carp, J., Park, J., Polk, T. A., & Park, D. C. (2011). Age differences in neural distinctiveness revealed by multi-voxel pattern analysis. *Neuroimage*, *56*(2), 736–743. https://doi.org/10.1016/j.neuroimage.2010.04.267

Chadwick, M. J., Bonnici, H. M., & Maguire, E. A. (2012). Decoding information in the human hippocampus: A user's guide. *Neuropsychologia*, *50*(13), 3107–3121. https://doi.org/10.1016/j.neuropsychologia.2012.07.007

Chen J, Leong Y Chang, Honey C J, Yong C H, Norman K A and Hasson U. (2017). Shared memories reveal shared structure in neural activity across individuals. Nat Neurosci, 20(1), 115–125. 10.1038/nn.4450

Chen, J., Leong, Y. C., Honey, C. J., Yong, C. H., Norman, K. A., & Hasson, U. (2017). Shared memories reveal shared structure in neural activity across individuals. *Nature Neuroscience*, *20*(1), 115–125. https://doi.org/10.1038/nn.4450

Cheriet, N., Folville, A., & Bastin, C. (2021). Shared event-memory for a public event in young and older adults. *Applied Cognitive Psychology*, *35*(4), 1035–1043. https://doi.org/10.1002/acp.3834

Choi, W., & Henderson, J. M. (2015). Neural correlates of active vision : An fMRI comparison of natural reading and scene viewing. *Neuropsychologia*, *75*(8), 109–118. https://doi.org/10.1016/j.neuropsychologia.2015.05.027

Comblain, C., D'Argembeau, A., & Van Der Linden, M. (2005). Phenomenal characteristics of autobiographical memories for emotional and neutral events in older and younger adults. *Experimental Aging Research*, *31*(2), 173–189. https://doi.org/10.1080/03610730590915010

Craik, F. I., & Rose, N. S. (2012). Memory encoding and aging: A neurocognitive perspective. *Neuroscience and Biobehavioral Reviews*, *36*(7), 1729–1739. https://doi.org/10.1016/j.neubiorev.2011.11.007

Deng, L., Davis, S. W., Monge, Z. A., Wing, E. A., Geib, B. R., Raghunandan, A., & Cabeza, R. (2021). Age-related dedifferentiation and hyperdifferentiation of perceptual and mnemonic representations. *Neurobiology of Aging*, *106*(10), 55–67. https://doi.org/10.1016/j.neurobiolaging.2021.05.021

Dennis, N. A., & Cabeza, R. (2015). Neuroimaging of Healthy Cognitive Aging. In *The Handbook of Aging and Cognition* (pp. 10–63). Psychology Press. https://doi.org/10.4324/9780203837665.ch1

Dimsdale-Zucker, H. R., & Ranganath, C. (2019). Representational similarity analyses: A practical guide for functional MRI applications. *Handbook of Behavioral Neuroscience*, *28*, 509–525. https://doi.org/10.1016/B978-0-12-812028-6.00027-6

Esposito, M. D., Deouell, L. Y., Gazzaley, A., Wheeler, H. H., & Brain, J. (2003). alterations in the bold fmri signal with ageing and disease: A challenge for neuroimaging groups of individuals rely heavily on the assumption of. *Nature Reviews Neuroscience*, *4*(November), 863–872. https://doi.org/10.1038/nrn1246

Folville A, Bahri M Ali, Delhaye E, Salmon E, D'Argembeau A and Bastin C. (2020). Age-related differences in the neural correlates of vivid remembering. NeuroImage, 206 116336 10.1016/j.neuroimage.2019.116336

Folville, A., Bahri, M. A., Delhaye, E., Salmon, E., D'Argembeau, A., & Bastin, C. (2020, November). Age-related differences in the neural correlates of vivid remembering. *NeuroImage*, *206*(2), 116336. https://doi.org/10.1016/j.neuroimage.2019.116336

Folville, A., D'Argembeau, A., & Bastin, C. (2020). Deciphering the relationship between objective and subjective aspects of recollection in healthy aging. *Memory*, *28*(3), 362–373. https://doi.org/10.1080/09658211.2020.1720741

Folville, A., Jeunehomme, O., Bastin, C., & D'Argembeau, A. (2020). The impact of age on the temporal compression of daily life events in episodic memory. *Psychology and Aging*, *35*(4), 484–496. https://doi.org/10.1037/pag0000456

Folville, A., Simons, J. S., D'Argembeau, A., & Bastin, C. (in press). I remember it like it was yesterday: Age-related differences in the subjective experience of remembering. *Psychonomic Bulletin & Review*. https://doi.org/10.3758/s13423-021-02048-y

Folville, A., Vandeleene, N., & Bastin, C. (2021). Shared event memory in aging : Across-participants similarity of vividness judgements decreases with age. *Aging, Neuropsychology, and Cognition*, 1–17. https://doi.org/10.1080/13825585.2021.1892578

Geerligs, L., & Campbell, K. L. (2018). Age-related differences in information processing during movie watching. *Neurobiology of Aging*, *72*(12), 106–120. https://doi.org/10.1016/j.neurobiolaging.2018.07.025

Hashtroudi, S., Johnson, M. K., & Chrosniak, L. D. (1990). Aging and qualitative characteristics of memories for perceived and imagined complex events. *Psychology and Aging*, *5*(1), 119–126. https://doi.org/10.1037/0882-7974.5.1.119

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject synchronization of cortical activity during natural vision. *Science*, *303*(March), 1634–1640. https://doi.org/10.1126/science.1089506

Hill, P. F., King, D. R., & Rugg, M. D. (2021). Age differences in retrieval-related reinstatement reflect age-related dedifferentiation at encoding. *Cerebral Cortex (New York, N.Y. : 1991)*, *31*(1), 106–122. https://doi.org/10.1093/cercor/bhaa210

Hirst, W., & Echterhoff, G. (2012). Remembering in conversations: The social sharing and reshaping of memories. *Annual Review of Psychology*, *63*(1), 55–79. https://doi.org/10.1146/annurev-psych-120710-100340

Humphreys, G. F., Ralph, M. A. L., Simons, J. S., & Schiavo, G. (2020). A unifying account of angular gyrus contributions to episodic and semantic cognition. *Trends in Neurosciences*, *43*(1), 1–21. https://doi.org/10.1016/j.tins.2021.01.006

Hutton C, Bork A, Josephs O, Deichmann R, Ashburner J and Turner R. (2002). Image Distortion Correction in fMRI: A Quantitative Evaluation. NeuroImage, 16(1), 217–240. 10.1006/nimg.2001.1054

Isola, P., Xiao, J., Torralba, A., & Oliva, A. (2011, June 20–25). *What makes an image memorable?* [Paper presentation]. IEEE Conference on Computer Vision and Pattern Recognition (CVPR), c, Colorado Springs, CO, USA (pp. 145–152). http://web.mit.edu/phillipi/www/publications/WhatMakesAnImageMemorable.pdf

Johnson, M. K., Hashtroudi, S., & Lindsay, D. S. (1993). Source monitoring. *Psychological Bulletin*, *114*(1), 3–28. https://doi.org/10.1037/0033-2909.114.1.3

Johnson, M. K., Kuhl, B. A., Mitchell, K. J., Ankudowich, E., & Durbin, K. A. (2015). Age-related differences in the neural basis of the subjective vividness of memories: Evidence from multivoxel pattern classification. *Cognitive, Affective & Behavioral Neuroscience*, *15*(3), 644–661. https://doi.org/10.3758/s13415-015-0352-9

Katsumi, Y., Andreano, J. M., Barrett, L. F., Dickerson, B. C., & Touroutoglou, A. (2021). Greater neural differentiation in the ventral visual cortex is associated with youthful memory in superaging. *Cerebral Cortex*, *31*(11), 5275–5287. https://doi.org/10.1093/cercor/bhab157

Kobelt, M., Sommer, V. R., Keresztes, A., & Werkle-bergner, M. (2021). Tracking age differences in neural distinctiveness across representational levels. *Journal of Neuroscience*, *41*(15), 1–39. https://doi.org/10.1523/JNEUROSCI.2038-20.2021

Koch, G. E., Paulus, J. P., & Coutanche, M. N. (2020). Neural patterns are more similar across individuals during successful memory encoding than during failed memory encoding. *Cerebral Cortex (New York, N.Y : 1991)*, *30*(7), 3872–3883. https://doi.org/10.1093/cercor/bhaa003

Koen, J. D., Hauck, N., & Rugg, M. D. (2019). The relationship between age, neural differentiation, and memory performance. *Journal of Neuroscience*, *39*(1), 149–162. https://doi.org/10.1523/JNEUROSCI.1498-18.2018

Koen, J. D., & Rugg, M. D. (2019). Neural dedifferentiation in the aging brain. *Trends in Cognitive Sciences*, *23*(7), 547–559. https://doi.org/10.1016/j.tics.2019.04.012

Koen, J. D., Srokova, S., & Rugg, M. D. (2020). Age-related neural dedifferentiation and cognition. *Current Opinion in Behavioral Sciences*, *32*(Figure 1), 7–14. https://doi.org/10.1016/j.cobeha.2020.01.006

Koutstaal, W. (2003). Older adults encode - But do not always use - Perceptual details: Intentional versus unintentional effects of detail on memory judgments. *Psychological Science*, *14*(2), 189–193. https://doi.org/10.1111/1467-9280.01441

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis - connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, *2*, 1–28. https://doi.org/10.3389/neuro.06.004.2008

LaPLume, A., Anderson, N. D., McKetton, L., Levine, B., & Troyer, A. K. (2021). When I'm 64: Age-related variability in over 40,000 online cognitive test takers. *Journal of Gerontology: Psychological Sciences*, *77*(1), 104–117. https://doi.org/10.1093/geronb/gbab143

Levine, B., Svoboda, E., Hay, J. F., Winocur, G., & Moscovitch, M. (2002). Aging and autobiographical memory: Dissociating episodic from semantic retrieval. *Psychology and Aging*, *17*(4), 677–689. https://doi.org/10.1037//0882-7974.17.4.677

Li, S. C., Lindenberger, U., & Frensch, P. A. (2000). Unifying cognitive aging: From neuromodulation to representation to cognition. *Neurocomputing*, *32*(33), 879–890. https://doi.org/10.1016/S0925-2312(00)00256-3

Li, S. C., Lindenberger, U., & Sikström, S. (2001). Aging cognition: From neuromodulation to representation. *Trends in Cognitive Sciences*, *5*(11), 479–486. https://doi.org/10.1016/S1364-6613(00)01769-1

Lindenberger, U. (2014). Human cognitive aging: Corriger la fortune?. *Science*, *346*(6209), 572–578. https://doi.org/10.1126/science.1254403

Machielsen, W. C. M., Rombouts, S. A. R. B., Barkhof, F., Scheltens, P., & Witter, M. P. (1999). FMRI of visual encoding: Reproducibility of activation. *NeuroImage*, *9*(6 PART II), 156–164. https://doi.org/10.1002/(SICI)1097-0193(200003)9:3<156::AID-HBM4>3.0.CO;2-Q

Marchewka, A., Żurawski, Ł., Jednoróg, K., & Grabowska, A. (2014). The Nencki Affective Picture System (NAPS): Introduction to a novel, standardized, wide-range, high-quality, realistic picture database. *Behavior Research Methods*, *46*(2), 596–610. https://doi.org/10.3758/s13428-013-0379-1

Marks, D. F. (1973). Visual imagery differences in the recall of pictures. *British Journal of Psychology*, *64*(1), 17–24. https://doi.org/10.1111/j.2044-8295.1973.tb01322.x

Mattis, S. (1976). Mental status examination for organic mental syndrome in the elderly patient. *Geriatric Psychiatry*.

McDonough, I. M., Cervantes, S. N., Gray, S. J., & Gallo, D. A. (2014). Memory's aging echo: Age-related decline in neural reactivation of perceptual details during recollection. *NeuroImage*, *98*(9), 346–358. https://doi.org/10.1016/j.neuroimage.2014.05.012

Merck, C., Yamashiro, J. K., & Hirst, W. (2020). Remembering the big game: Social identity and memory for media events. *Memory*, *28*(6), 1–20. https://doi.org/10.1080/09658211.2020.1784232

Mitchell, K. J., & Hill, E. M. (2019). The impact of focusing on different features during encoding on young and older adults' source memory. *Open Psychology*, *1*(1), 106–118. https://doi.org/10.1515/psych-2018-0008

Mitchell, K. J., & Johnson, M. K. (2009). Source monitoring 15 years later: What have we learned from fMRI about the neural mechanisms of source memory?. *Psychological Bulletin*, *135*(4), 638–677. https://doi.org/10.1037/a0015849

Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, *10*(9), 424–430. https://doi.org/10.1016/j.tics.2006.07.005

Nyberg, L. (2017). Functional brain imaging of episodic memory decline in ageing. *Journal of Internal Medicine*, *281*(1), 65–74. https://doi.org/10.1111/joim.12533

Nyberg, L., Lövdén, M., Riklund, K., Lindenberger, U., & Bäckman, L. (2012). Memory aging and brain maintenance. *Trends in Cognitive Sciences*, *16*(5), 292–305. https://doi.org/10.1016/j.tics.2012.04.005

Oedekoven, C. S. H., Keidel, J. L., Berens, S. C., & Bird, C. M. (2017). Reinstatement of memory representations for lifelike events over the course of a week. *Scientific Reports*, *7*(1), 1–12. https://doi.org/10.1038/s41598-017-13938-4

Oosterhof N N, Connolly A C and Haxby J V. (2016). CoSMoMVPA: Multi-Modal Multivariate Pattern Analysis of Neuroimaging Data in Matlab/GNU Octave. Front. Neuroinform., 10 10.3389/fninf.2016.00027

Pedraza, O., Lucas, J. A., Smith, G. E., Petersen, R. C., Graff-Radford, N. R., & Ivnik, R. J. (2010). Robust and expanded norms for the dementia rating scale. *Archives of Clinical Neuropsychology*, *25*(5), 347–358. https://doi.org/10.1093/arclin/acq030

Piolino, P., Coste, C., Martinelli, P., Macé, A., Quinette, P., Guillery-Girard, B., & Belleville, S. (2010). Reduced specificity of autobiographical memory and aging: Do the executive and feature binding functions of working memory have a role ? *Neuropsychologia*, *48*(2), 429–440. https://doi.org/10.1016/j.neuropsychologia.2009.09.035

Rissman, J., Gazzaley, A., & D'Esposito, M. (2004). Measuring functional connectivity during distinct stages of a cognitive task. *NeuroImage*, *23*(2), 752–763. https://doi.org/10.1016/j.neuroimage.2004.06.035

Ritchey, M., & Cooper, R. A. (2020). Deconstructing the posterior medial episodic network. *Trends in Cognitive Sciences*, *24*(6), 451–465. https://doi.org/10.1016/j.tics.2020.03.006

Ritchey, M., Wing, E. A., Labar, K. S., & Cabeza, R. (2013). Neural similarity between encoding and retrieval is related to memory via hippocampal interactions. *Cerebral Cortex*, *23*(12), 2818–2828. https://doi.org/10.1093/cercor/bhs258

Robin, J., & Moscovitch, M. (2017). Familiar real-world spatial cues provide memory benefits in older and younger adults. *Psychology and Aging*, *32*(3), 210–219. https://doi.org/10.1037/pag0000162

Rubin, D. C., & Schulkind, M. D. (1997). Distribution of important and wordcued autobiographical memories. *Psychology and Aging*, *20*(3), 524–535. https://doi.org/10.1037/0882-7974.12.3.524

Rugg, M. D., Johnson, J. D., & Uncapher, M. R. (2015). Encoding and Retrieval in Episodic Memory. *The Wiley Handbook on the Cognitive Neuroscience of Memory*, 84–107. https://doi.org/10.1002/9781118332634.ch5

Schacter, D. L., Kaszniak, A. W., Kihlstrom, J. F., & Valdiserri, M. (1991). The relation between source memory and aging. *Psychology and Aging*, *6*(4), 559–568. https://doi.org/10.1037/0882-7974.6.4.559

Schlagman, S., Kliegel, M., Schulz, J., & Kvavilashvili, L. (2009). Differential effects of age on involuntary and voluntary autobiographical memory. *Psychology and Aging*, *24*(2), 397–411. https://doi.org/10.1037/a0015785

St-Laurent, M., Abdi, H., Bondad, A., & Buchsbaum, B. R. (2014). Memory reactivation in healthy aging: Evidence of stimulus-specific dedifferentiation. *Journal of Neuroscience*, *34*(12), 4175–4186. https://doi.org/10.1523/JNEUROSCI.3054-13.2014

St-Laurent, M., Buchsbaum, B. R., & Anderson, N. (2019). How multiple retrievals affect neural reactivation in young and older adults. *The Journals of Gerontology. Series B, Psychological Sciences and Social Sciences*, *74*(7), 1086–1100. https://doi.org/10.1093/geronb/gbz075

St. Jacques, P. L., & Levine, B. (2007). Ageing and autobiographical memory for emotional and neutral events. *Memory*, *15*(2), 129–144. https://doi.org/10.1080/09658210601119762

Tibon, R., Fuhrmann, D., Levy, D. A., Simons, J. S., & Henson, R. N. (2019). Multimodal integration and vividness in the angular gyrus during episodic encoding and retrieval. *Journal of Neuroscience*, *39*(22), 4365–4374. https://doi.org/10.1523/JNEUROSCI.2102-18.2018

Trelle, A. N., Henson, R. N., & Simons, J. S. (2019). Neural evidence for age-related differences in representational quality and strategic retrieval processes. *Neurobiology of Aging*, *84*(12), 50–60. https://doi.org/10.1016/j.neurobiolaging.2019.07.012

Tulving, E. (1972). Episodic and semantic memory. *Organization of Memory*, 381–403.

Verhaeghen, P., & Marcoen, A. (1993). More or less the same? A memorability analysis on episodic memory tasks in young and older adults. *Journals of Gerontology*, *48*(4), 172–178. https://doi.org/10.1093/geronj/48.4.P172

West, K. L., Zuppichini, M. D., Turner, M. P., Sivakolundu, D. K., Zhao, Y., Abdelkarim, D., Spence, J. S., & Rypma, B. (2019). NeuroImage BOLD hemodynamic response function changes signi fi cantly with healthy aging. *NeuroImage*, *188*(December 2018), 198–207. https://doi.org/10.1016/j.neuroimage.2018.12.012

Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(20), 11125–11129. https://doi.org/10.1073/pnas.97.20.11125

Wing, E. A., Ritchey, M., & Cabeza, R. (2015). Reinstatement of individual past events revealed by the similarity of distributed activation patterns during encoding and retrieval. *Journal of Cognitive Neuroscience*, *27*(4), 679–691. https://doi.org/10.1162/jocn_a_00740

Xiao, X., Zhou, Y., Liu, J., Ye, Z., Yao, L., Zhang, J., Chen, C., & Xue, G. (2020). Individual-specific and shared representations during episodic memory encoding and retrieval. *NeuroImage*, *217*(8), 116909. https://doi.org/10.1016/j.neuroimage.2020.116909

Yazar, Y., Bergström, Z. M., & Simons, J. S. (2017). Reduced multimodal integration of memory features following continuous theta burst stimulation of angular gyrus. *Brain Stimulation*, *10*(3), 624–629. https://doi.org/10.1016/j.brs.2017.02.011

Zadbood, A., Chen, J., Leong, Y. C., Norman, K. A., & Hasson, U. (2017). How we transmit memories to other brains: Constructing shared neural representations via communication. *Cerebral Cortex*, *27*(10), 4988–5000. https://doi.org/10.1093/cercor/bhx202

Zaromb, F., Butler, A. C., Agarwal, P. K., & Roediger, H. L. (2014). Collective memories of three wars in United States history in younger and older adults. *Memory & Cognition*, *42*(3), 383–399. https://doi.org/10.3758/s13421-013-0369-7

Zheng, L., Gao, Z., Xiao, X., Ye, Z., Chen, C., & Xue, G. (2018). Reduced fidelity of neural representation underlies episodic memory decline in normal aging. *Cerebral Cortex (New York, N.Y. : 1991)*, *28*(7), 2283–2296. https://doi.org/10.1093/cercor/bhx130