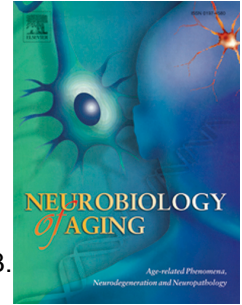


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Neural correlates of durable memories across the adult lifespan: brain activity at encoding and retrieval

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1 **Neural correlates of durable memories across the adult lifespan: brain activity**
2 **at encoding and retrieval**

3
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16

17

18 **Abstract:**

19 Age-related effects on brain activity during encoding and retrieval of episodic memories are well
20 documented. However, research typically tests memory only once, shortly after encoding. Retaining
21 information over extended periods is critical, and there are reasons to expect age-related effects on
22 the neural correlates of durable memories. Here we tested whether age was associated with the
23 activity elicited by durable memories. 143 participants (22-78 years) underwent an episodic memory
24 experiment where item-context relationships were encoded and tested twice. Participants were
25 scanned during encoding and the first test. Memories retained after 90 minutes but later forgotten
26 were classified as transient, while memories retained after 5 weeks were classified as durable.
27 Durable memories were associated with greater encoding activity in inferior lateral parietal and
28 posteromedial regions and greater retrieval activity in frontal and insular regions. Older adults
29 exhibited lower posteromedial activity during encoding and higher frontal activity during retrieval,
30 possibly reflecting greater involvement of control processes. This demonstrates that long-lasting
31 memories are supported by specific patterns of cortical activity that are related to age.

32

33 **Keywords:**

34 Aging; fMRI; encoding; episodic memory; retrieval; durable memory.

35

36

37 1. Introduction

38 Despite the extensive literature on neurocognitive aging of memory, no study has focused on the
39 brain correlates of long-lasting memories. It is well known that some events can be remembered
40 after extended periods of time while other memories quickly fade or are even forgotten. Yet, most
41 research tests memory just once, typically during the same day, remaining blind to key processes
42 linked to the creation of long-lasting, durable memories. Thus, we lack knowledge about how older
43 adults encode and retrieve such durable memories compared to younger adults. Here we tested
44 whether activity patterns specific to durable -relative to transient- memory were affected by age,
45 both at encoding and at retrieval. Participants completed an episodic memory task where item-
46 context (source memory) associations were implicitly encoded and tested twice, after ≈ 90 minutes
47 and ≈ 5 weeks. By repeated testing of the same stimuli, durable memories were distinguished from
48 memories initially retrieved but later forgotten (transient memories). Functional magnetic resonance
49 imaging (fMRI) data during the encoding and the short delay retrieval sessions were collected to
50 identify the specific patterns of activity associated with subsequent durable memories and their
51 association with age.

52

53 Age is associated with a marked reduction in episodic memory function (Nyberg et al., 2012;
54 Rönnlund et al., 2005) and changes in activity patterns supporting memory formation and retrieval
55 (Davis et al., 2008; Grady, 2012; Maillet and Rajah, 2014). A much-used approach in memory
56 research is the subsequent memory paradigm. Subsequent memory paradigms contrast stimulus
57 encoding activity between trials that are later remembered versus those that are forgotten. Research
58 using this paradigm has identified successful memory with increased activity in widespread cortical
59 areas as well as in the hippocampus, and decreased activity in Default-Mode Network (DMN) regions
60 (Kim, 2011; Spaniol et al., 2009). Decreased activity in task-positive and reduced deactivation in task-
61 negative areas are the most characteristic features of successful memory encoding in older adults

62 when tested at short intervals (Maillet and Rajah, 2014; Wang and Cabeza, 2016). The parieto-
63 occipital cortex, involved visuospatial processing (Dennis et al., 2007; Park et al., 2013), together with
64 the prefrontal cortex (Dennis et al., 2008; Miller et al., 2008) consistently exhibit lower encoding-
65 related activity with higher age. Lower subsequent memory effects in older adults may arise from a
66 reduced ability to allocate neural resources into relevant memory and attentional networks. Thus,
67 based on evidence that tested older adults' memory after short delays, we hypothesized that with
68 higher age, participants would show less activity associated with durable memories. Specifically, we
69 expected age-related differences in core encoding regions such as in parieto-occipital and prefrontal
70 regions, reflecting compromised encoding mechanisms. When compared with the patterns of activity
71 supporting transient memories, the neural correlates supporting durable memory encoding would be
72 less distinct in aging. For memory retrieval, different activity patterns have repeatedly been reported
73 with advancing age (Addis et al., 2014; Angel et al., 2013; Cansino et al., 2015; but see Wang et al.,
74 2016). During the retrieval of context memories, higher frontal activity emerges as a recurrent
75 finding (Dulas and Duarte, 2012; Leshikar and Duarte, 2014; Morcom et al., 2007), allegedly reflecting
76 increased retrieval effort in older adults. In addition, age-related differences in retrieval activity
77 might interact with testing effects as more effortful retrieval increases the benefit of testing effects
78 (Wing et al., 2013). Consequently, we hypothesized older adults would exhibit higher frontal activity
79 when retrieving durable memories.

80

81 Further, we aimed to expand the current knowledge on the neural correlates sustaining durable
82 memories at encoding and retrieval with the largest sample of participants to date. For encoding, we
83 envisioned three possible scenarios. First, durable memories could be represented by an extension of
84 the activity-based principle governing initial memory success. Compared to transient memories, long-
85 lasting memories would be characterized by increased levels of activity in the same regions that
86 support initial memory. Second, durable memories could rely on an activity-based principle but on
87 different networks than those sufficient for initial memory formation. If this scenario is true, the

88 blood-oxygen-level dependent (BOLD) signal will reflect increased likelihood of an item being
89 available for a long period of time but in areas not typically associated with encoding success. Both
90 scenarios are not necessarily in conflict. Finally, durable memories could be undistinguishable at
91 encoding or rely on additional mechanisms and thus appear unrelated to the degree of cortical
92 activity during encoding.

93

94 The available evidence points in different directions. Most studies found that durable memories were
95 associated with increased activity in the memory encoding network such as medial temporal,
96 prefrontal and parietal regions (Uncapher and Rugg, 2005; Wagner et al., 2016), including the
97 hippocampus (Carr et al., 2010). Additionally, frontal and posteromedial encoding activity has
98 specifically been linked to memory durability (Liu et al., 2014; Uncapher and Rugg, 2005) as well as
99 the amygdala when emotional stimuli were considered (Ritchey et al., 2008). Memory durability has
100 also been associated with factors other than encoding strength, such as hippocampal-neocortical
101 connectivity (Sneve et al., 2015), possibly related to post-encoding system consolidation processes,
102 or encoding similarity, mostly in DMN regions (Wagner et al., 2016).

103

104 The same three general scenarios described for encoding were also considered for retrieval. The only
105 existing report on retrieval activity of durable memories showed increased activity in posteromedial,
106 occipital and fusiform areas during durable versus transient memories (Wagner et al., 2016). The
107 results to some degree overlapped with the “core recollection network” (Johnson and Rugg, 2007),
108 and with areas related to retrieval success of visually encoded material, i.e. in partial agreement with
109 the overlapping scenario suggested above. Additionally, when the material is tested twice, as in the
110 present study, there might be benefits from retrieval practice (Carpenter et al., 2008; Rowland and
111 DeLosh, 2015). Thus, the initial, short delay retrieval is also a process by which item-context
112 associations can be strengthened. Testing effects seem to be contingent on processes that support

113 memory success at encoding (Liu and Reder, 2016; Wing et al., 2013). Thus at retrieval, durable
114 memory activity in regions involved in cognitive control –such as in anterior cingulate, frontal and
115 insular cortices- could be considered evidence in support of memory-strength modifying re-encoding
116 processes.

117

118 Hence, in the present study, participants implicitly encoded source memory associations that were
119 later tested twice, in a short and a long delay retrieval. The main goal was to identify cortical patterns
120 of activity at encoding and at the short-delay retrieval specifically associated with long-lasting
121 memories and test whether such patterns of activity varied as a function of age.

2. Material and methods

2.1 Participants

One hundred and forty-three participants (females = 90, mean age = 51.0 [standard deviation (SD) = 15.8], age range = 22-78) were included in the final sample. All participants completed the experimental design that included one incidental episodic encoding task and two retrieval tests. All participants were scanned during encoding and the first retrieval task. All participants were screened through health and neuropsychological interviews (see **Supplementary Information**; see **Table 1** for main neuropsychological and sociodemographic variables). Participants were also excluded on the basis of bad quality or incomplete MRI data (n = 12), long retrieval span ≥ 90 days (n = 15) or insufficient numbers of items belonging to a given experimental condition (n = 14; < 8 items belonging to any condition of interest). All participants gave written informed consent, and the study was approved by the Regional Ethical Committee of South Norway. Data were independent of an earlier report by our group (Sneve et al., 2015). Participants were compensated for their participation.

[Insert Table 1 about here]

2.2 Experimental design

The stimulus material consisted of 300 black and white line drawings depicting everyday objects and items. The experiment consisted of an incidental encoding task and two tests; one after a short interval (≈ 90 minutes) and the other after, on average, 34.1 (SD = 15.8) days. The main experimental design has been thoroughly described elsewhere (Sneve et al., 2015). Briefly, the encoding and the first –but not the long-delay– retrieval task took place in the MRI scanner. The encoding and the retrieval tasks consisted of two and four runs, respectively, that included 50 trials each. All runs

148 started and ended with an 11 s baseline recording period in which a central fixation cross was
149 present. An additional baseline period was also presented once in the middle of each run. In the
150 encoding runs, a trial started with a voice asking into the participant's headphones, either "Can you
151 eat it?" or "Can you lift it?" (in Norwegian, **Figure 1_a**). Each question was asked 25 times in each run
152 in a pseudorandomized order. One second after question onset, a picture of an item appeared on the
153 screen together with a response indicator that instructed the participant which button to press to
154 respond "Yes" or "No" to the previous questions. Button-response mapping was counterbalanced
155 across subjects. The subject had 2 s to produce a response before the object was replaced by a
156 central fixation cross which remained on the screen throughout the intertrial interval, that lasted
157 between 1-7 s (exponential distribution over four discrete intervals; mean duration = 2.98 [SD 2.49]
158 s).

159
160 Participants were asked to perform two surprise memory tests. The first one took place inside the
161 MRI scanner approximately 1.5 hours after the last encoding trial. The long-delay retrieval session
162 occurred \approx 5 weeks after the encoding, when participants returned to the experimental laboratory
163 for a debrief meeting. All encoding trials were presented in both retrieval sessions. Test trials started
164 with a recorded voice asking the following (Question 1): "Have you seen this item before" (**Figure 1_b**).
165 Then, a picture of an item appeared on the screen, and the participant was instructed to indicate Yes
166 (seen) or No (not seen) with a button press. In each run, 25 old items (presented during encoding)
167 and 25 new items (not presented during encoding) were presented in a pseudorandomized order.
168 Each object stayed on the screen for 2 s; if the participant responded that the item was new or did
169 not respond, the trial ended. When the participant remembered seeing the item (pressed Yes), a new
170 question followed (Question 2): "Can you remember what you were supposed to do with the item?".
171 A No response ended the trial, whereas a Yes response, indicating that the participant also
172 remembered the action associated with the item during the encoding, was followed by a final control
173 question (Question 3): "Were you supposed to eat it or lift it?". Here, the participant got a two-

174 alternative forced choice between the two encoding actions “Eat” or “Lift” (I was supposed to judge
175 whether it would be possible to eat/lift it). Note that the specific questions asked during scanning
176 were simplified to fit within the temporal limits of the paradigm, but that all participants were
177 instructed in detail before the test session that the questions pertained to the item-action evaluation
178 performed at encoding.

179

180

[Insert Figure 1 about here]

181

182 **2.3 Behavioral analysis**

183

184 Each test trial response to old items was behaviorally classified as follows: (1) source memory (Yes
185 response to Question 1 and 2 and correct response to Question 3); (2) item memory (correct Yes
186 response to Question 1 and either a No response to Question 2, or incorrect response to Question 3);
187 or (3) miss (incorrect No response to Question 1). New items were classified either as (4) correct
188 rejections or (5) false alarms (see **Table 2** for behavioral results in each test session). To estimate
189 memory performance strength, we additionally corrected the number of source memory trials by the
190 number of incorrect source judgments (correct answers in Question 3 - incorrect answers in Question
191 3). This correction tentatively accounts for processes such as false memories, threshold criteria in
192 Question 2 or guessing behavior that affects the raw estimates of source memory performance. Test
193 trial responses in both retrieval tests were combined to create the fMRI behavioral conditions
194 (described in section **2.6 fMRI analysis**).

195

196 All non-vertex-wise statistical analyses were performed in R-environment ([https://www.r-](https://www.r-project.org/)
197 [project.org/](https://www.r-project.org/); v.3.2.5). We did not find strong support for a non-linear relationship between age and
198 memory performance as assessed with the Bayesian information criterion (BIC). Thus, only the linear
199 effects of age were tested in subsequent analysis. The association between age and behavioral and

200 neuropsychological data was tested with general linear models (GLMs) with age and sex as predictors.
201 Statistical significance was considered at $p < 0.05$, if not otherwise stated, and Bonferroni corrections
202 were applied when appropriate. When not explicitly specified, data refers to mean (SD) and error
203 bars to standard errors of the mean. Proportions are considered with respect to the new and old
204 items as pertinent (e.g. source vs. old trials; false alarms vs. new trials).

205

206 **2.4 MRI acquisition**

207

208 Imaging data were collected using a 24-channel Siemens head coil on a 3T MRI (Siemens Skyra
209 scanner, Siemens Medical Solutions, Germany) at Rikshospitalet, Oslo University Hospital. The
210 functional imaging parameters were equivalent across all fMRI runs: 43 transversally oriented slices
211 (no gap) were measured using a BOLD-sensitive T2*-weighted EPI sequence (TR = 2390 ms, TE = 30
212 ms, flip angle = 90° ; voxel size = 3 x 3 x 3 mm; FOV = 224 x 224 mm; interleaved acquisition;
213 generalized autocalibrating partially parallel acquisitions acceleration factor = 2). Each encoding run
214 produced 131 volumes while the mean number of volumes per retrieval run was 208. At the start of
215 each fMRI run, three dummy volumes were collected to avoid T1 saturation effects in the analyzed
216 data. Anatomical T1-weighted MPRAGE images consisting of 176 sagittally oriented slices were
217 obtained using a turbo field echo pulse sequence (TR = 2300 ms, TE = 2.98 ms, flip angle = 8° , voxel
218 size = 1 x 1 x 1 mm, FOV = 256 x 256 mm). Visual stimuli were presented in the scanner environment
219 with a 32-inch monitor while participants responded using the ResponseGrip device (both
220 NordicNeuroLab, Norway). Auditory stimuli were presented to the participants' headphones through
221 the scanner intercom.

222

223 **2.5 MRI data preprocessing**

224

225 Cortical reconstruction and volumetric segmentation of the T1-weighted scans were performed with
226 FreeSurfer 5.3 pipeline (<http://surfer.nmr.mgh.harvard.edu/fswiki>), thoroughly described elsewhere
227 (Dale et al., 1999; Fischl et al., 1999; Fischl and Dale, 2000). Briefly, the automatized processing
228 pipeline includes removal of non-brain tissue, Talairach transformation, intensity correction, tissue
229 segmentation, and cortical surface reconstruction. Functional imaging data from the memory tasks
230 was preprocessed using the Freesurfer Functional Analysis Stream (FSFAST;
231 <https://surfer.nmr.mgh.harvard.edu/fswiki/FsFast>). After correction of functional images for
232 distortions caused by B0 inhomogeneities in EPI scans, the images were motion corrected, slice
233 timing corrected to the middle of each volume's TR, intensity normalized, and registered to each
234 participant's anatomical volume. Then, each functional dataset was resampled to a common space
235 using a surface-based intersubject registration, bringing cortical hemispheres into *fsaverage* average
236 space. After running first-level GLM analysis (see section **2.6 fMRI analysis**), surface smoothing was
237 applied using a Gaussian kernel of 8 mm full-width half-maximum (FWHM) and each participant's
238 surface map was introduced to a higher-level GLM analysis.

239

240 **2.6 fMRI analysis**

241

242 *Main effects of memory contrasts*

243 A first-level GLM consisting of the conditions of interest with onsets and durations corresponding to
244 the experimental trial period (2s) was set up for each encoding and retrieval run and was convolved
245 with a two-gamma canonical hemodynamic response function (HRF). Each event was assigned to a
246 condition based on the participant's response to a given item during the test sessions. The
247 experimental conditions were created by combining trial responses in both the short delay and the
248 long delay tests (see section **2.2 Experimental design** and **2.3 Behavioral analysis**) were defined as
249 follows: 1) durable memory (DM) condition that consisted of items that were correctly identified
250 with context information in both the short and long delay retrieval tests –correct Question 3 in both

251 tests; 2) transient memory condition (TM), that included those trials where the participant could
252 correctly identify the item with context information in the first retrieval test but not in the second
253 (long-delay) retrieval –correct Question 3 in the short delay test but not in the long delay test- and; 3)
254 Item (IM) memory condition that consisted of those items that were correctly recognized in the short
255 delay retrieval but without (or with incorrect) context information –correct Question 1, but not
256 Question 3, in the short delay test- (**Figure 1d**). The later condition-of-interest was only based on the
257 first retrieval. In addition, several regressors were included to soak up BOLD variance associated with
258 miss response trials and trials with no response. Four further regressors were added in the retrieval
259 runs exclusively, modeling the second and the third test questions as well as false alarms and correct
260 rejections associated with the presentation of the new items. In addition to the task regressors and
261 their temporal derivatives, estimated motion correction parameters and a set of polynomials (up to
262 the second degree) were included in the first-level GLM as nuisance regressors. The model and the
263 data were high-pass filtered at 0.01 Hz, and temporal autocorrelations in the residuals were
264 corrected using a prewhitening approach. For each individual, two contrasts of parameter estimates
265 were computed for further statistical analysis: DM versus TM conditions (durable memory contrast)
266 and DM and TM trials versus IM (initial memory success contrast). To compute the latter contrast, we
267 ran a separate first-level model in which a single regressor included both the DM and the TM trials.
268 For fMRI analysis, on average 19.0 (8.3) memory trials were classified as durable memories, 31.5
269 (11.4) as transient memories and 23.1 (8.4) as item memories.

270

271 Next, individual contrasts were introduced into group level ordinary least square GLM analysis to
272 explore the main contrast effects. All statistical models additionally included sex and age as
273 covariates (unless age was used as a variable of interest, see below). Statistical significance was
274 tested at each cortical vertex and the resulting maps were corrected for multiple comparisons using a
275 cluster-based approach; vertices were thresholded at $p < 0.01$ and the remaining clusters were
276 tested through permutation inference across 10,000 iterations using PALM scripts

277 (<http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/PALM>; Winkler et al., 2014). Cluster significance was considered
278 at a Family-Wise Error (FWE)-corrected level of $p < 0.05$ (two-sided). The encoding and the retrieval
279 fMRI data were independently processed. The reported results were robust to variations of the
280 cluster-formation threshold (**Supplementary Figures 1, 2**).

281

282 *Age-related effects on durable and initial memory contrasts*

283 The abovementioned higher-order GLM analysis was additionally used to explore the effects of age
284 on the memory contrasts. To better understand the age modulation over the memory contrasts, we
285 extracted the mean signal change from the FWE-corrected clusters. The fitted signal change was
286 assessed at age = ± 1 SD and 99% confidence intervals (CI) were computed to better interpret the
287 contrast direction.

288

289 *Relationship between durable and initial memory contrasts*

290 The cortical patterns of activation associated with durable memories were compared to those
291 associated with initial memory success, and to those reported in the literature through meta-
292 analytical contrast maps. Meta-analytical contrasts mainly included studies that tested participant's
293 memory after short periods of time (Kim, 2016, 2011). The map comparison was performed twofold:
294 First, the cortical patterns of activity associated with the durable memories were compared to those
295 associated with an initial memory success; thus we assessed the degree of anatomical overlapping
296 between the two memory contrasts. Cortical signal change maps associated with durable memory
297 and initial memory success contrasts -i.e. durable versus transient memories and source versus item
298 memory defined in the short-delay test- were used to assess the spatial correspondence between
299 both contrasts. Second, the durable memory and initial memory success signal change maps were
300 compared to published meta-analytical contrast maps of memory success both during encoding (Kim,

2011) and retrieval (Kim, 2016). The reader is addressed to the original studies (Kim, 2016, 2011) for details on meta-analytical methods and on the specific study selection criteria. Note that the meta-analytical contrasts only included memory success contrasts, in which activity for memory success items was compared with activity associated to memory failure. The meta-analysis though included a variety of studies, that were not necessarily constrained to source memory paradigms. We used a published meta-analysis –instead of an approach based on open databases- to avoid lexical confusions, select uniquely memory success contrasts and, isolate positive from negative activations. Activation likelihood estimation (ALE) maps were registered to the *fsaverage* template space, projected at mid surface using the *mri_vol2surf* tool and compared to the memory maps resulting from the present study. For each type of contrast estimates, data were merged across hemispheres, Z-standardized and fed to random subsampling statistical analysis. To avoid collinearity between adjacent vertices, subsets of vertices (1000 vertices) were randomly selected and bivariate Pearson's correlations between the different memory contrasts were computed within these subsets of vertices. This process was iteratively repeated ($n = 5000$). The mean correlation of all the iterations was selected as the index representing the spatial overlap between memory contrasts. The analysis was performed independently for those contrasts representing encoding and retrieval. Additionally, initial memory success and durable memory significance maps, both at encoding and at retrieval, were binarized at $p < 0.01$ (uncorrected). Regions with unique or common patterns of activity were overlaid onto semi-inflated surfaces (**Figure 4 c,d**).

320

321

322 *Hippocampal analysis*

323 In addition to the surface-based analysis, contrast estimates were extracted from the left and right
324 hippocampal ROIs –in the original functional space-, based on the automatic subcortical
325 segmentation implemented in FreeSurfer (Fischl et al., 2002), to explore whether hippocampal

326 activity was related to memory success as well as any effect of age. The relationship between
327 hippocampal activity and durable memory and initial memory success estimates was tested
328 independently with four mixed-effect ANCOVAs that included hemisphere, behavioral condition, age,
329 and sex as independent variables. The different tests corresponded to encoding and retrieval data
330 and initial memory success (behavioral condition levels: source and item memory during the first
331 retrieval) and durable memory (behavioral condition levels: durable and transient memories)
332 estimates.

333

334 *Content-specific retrieval activity within the sensorimotor cortex*

335 As durable memories were characterized by higher retrieval activity within the sensorimotor cortex,
336 we conducted a post hoc analysis to test whether sensorimotor patterns of activity varied according
337 to the content of what was retrieved. That is, we studied whether content-specific patterns of
338 activity corresponded to the different source questions (“can you eat/lift it?”). Briefly, the behavioral
339 conditions of interest were redefined based on the short delay retrieval: 1) correct source memory
340 for items presented in association with the source *Eat* question (source-eat memory); 2) correct
341 source memory for items presented together with the source *Lift* question (source-lift memory) and,
342 3) item memory trials. fMRI data was preprocessed as described above (section **2.5 MRI data**
343 **preprocessing**). For each participant, the following contrasts of parameter estimates were computed
344 for further statistical analysis: source-eat versus item memory (eat memory contrast) and source-lift
345 versus item memory (lift memory contrast). GLM group-level analyses were carried out within the
346 sensorimotor strip. Content-specific activity was defined by inclusively masking vertices with
347 significant activity for one source question ($p < 1.0e^{-4}$) and exclusively masking for the alternative
348 contrast ($p < 0.01$). Clusters of >100 vertices were considered significant. See **Supplementary**
349 **Information** for further information.

350 **3. Results**

351

352 *Behavioral results*

353 After correcting for the number of incorrect source memories (correct answer in Question 3 -
354 incorrect answer in Question 3) the proportion of source memory trials was 0.40 (0.18) and 0.10
355 (0.08) for the short and long interval memory tests, respectively, in both cases significantly above
356 chance ($t = 27.1$ [$p < 2.2e^{-16}$] and $t = 12.9$ [$p < 2.2e^{-16}$] respectively; one-sample t-tests against 0). In
357 both retrieval tests, corrected source memory was negatively related to age ($t = -5.8$ [$p = 5.0e^{-8}$] and t
358 $= -4.9$ [$p = 2.4e^{-6}$]). Education level was not significantly associated with age nor with source memory
359 performance at short and at long delay tests (analysis of variance; $p > 0.05$; Supplementary Table 3).
360 See **Table 2** for behavioral results in each retrieval session and the effects of age on memory
361 performance. The proportion of items with source memory in the first retrieval that was also
362 retrieved with source during the second retrieval (durable memories) was .39 (.14). The remaining
363 items were classified either as miss or as invalid, due to no response. Age was positively associated
364 with the number of miss trials (in the first retrieval; $t = 3.8$ [$p = 2.1e^{-4}$]) and negatively related to the
365 number of transient memory items ($t = -3.6$ [$p = 4e^{-4}$]). Notably, age was unrelated to the proportion
366 of forgotten items between tests and the number of durable memory items (see **Table 3**; Bonferroni
367 corrected for the number of behavioral tests at $p < 0.01$ [$0.05/5$]). See also Supplementary Tables 3
368 and 4 for behavioral and neuropsychological data sampled into age groups.

369

370

[Insert Table 2 about here]

371

372

[Insert Table 3 about here]

373

374 *Main effects of memory contrasts*

375 Cortical vertex-wise analyses on BOLD signal were performed for encoding and retrieval fMRI to
376 identify the areas in which neural activity was related to initial memory success and to durable
377 memory (multiple comparisons corrected). The initial memory success contrast –source versus item
378 memory during the first retrieval– was associated with activity in widespread areas across the
379 cortical mantle, showing encoding and retrieval patterns similar to those previously reported in the
380 literature (Kim, 2016, 2011).

381

382 *Encoding activity.* During encoding, increased activity for initial memory success was found in large
383 left-lateralized prefrontal, inferior and medial temporal and parieto-occipital regions (**Figure 2a**).
384 Activity in the bilateral posteromedial and the right inferior parietal cortex was associated with
385 memory failure. During encoding, durable memories were associated with higher activity than
386 transient memories in a bilateral posteromedial cluster that encompassed the lingual and the
387 retrosplenial cortices, and in a left inferior parietal cluster (**Figure 2b**).

388

389 *Retrieval activity.* During the first retrieval, initial memory success was associated with higher activity
390 in widespread areas of the cortical mantle, especially in posteromedial, occipital and medial
391 prefrontal regions (**Figure 3a**), and reduced activity in restricted right medial superior frontal and
392 lateral orbitofrontal areas. During retrieval, durable memories were associated with increased
393 activity in the left sensorimotor cortex, the left insula and the right superior medial frontal cortex
394 (**Figure 3b**). See **Supplementary Table 1** for cluster stats and **Supplementary Figure 1 and 2** for the
395 cortical maps corrected at different cluster-forming thresholds. See **Supplementary Figure 3** for

396 activity associated with memory success during the second retrieval, regardless of behavioral
397 classification at the first retrieval.

398

399 *[Insert Figure 2 about here]*

400 *[Insert Figure 3 about here]*

401

402 *Spatial overlap between memory contrasts maps*

403 The mean spatial overlap between the durable contrast and the initial memory success map was $r =$
404 0.36 (0.02) for encoding and 0.36 (0.02) for retrieval suggesting moderate relationships between
405 both maps (Cohen, 1988). Next, these maps were compared with meta-analytical memory maps,
406 thus avoiding the overlap derived from the identical nature of the task. The spatial overlap between
407 initial memory success and meta-analytical memory maps was 0.29 (0.02) for encoding and 0.12
408 (0.02) for retrieval, showing small-to-medium and small anatomical correspondence with the meta-
409 analytical results. In contrast, the spatial correspondence between durable memory and meta-
410 analytical memory maps was trivial, both for encoding 0.08 (0.02) and retrieval 0.04 (0.02). Though
411 exhibiting a similar general pattern, the spatial overlap between maps was slightly higher when the
412 analyses were computed with durable memory and initial memory success contrast maps obtained
413 only from a subsample of young participants (below 40 years; see **Supplementary Information**). See
414 **Figure 4** for a graphical representations of the spatial overlap.

415

416 *[Insert Figure 4]*

417

418 *Age-related effects on durable memory and initial memory success contrasts*

419 Age was negatively related to posteromedial activity during the encoding of durable versus transient
420 memories in a cluster centered in the retrosplenial cortex, extending also to adjacent posterior
421 cingulate and precuneus regions (**Figure 5a**). Post hoc analyses revealed that young participants
422 exhibited higher activity in this posteromedial region for durable compared to transiently
423 remembered memories, while older adults showed no significant differences between conditions
424 (mean [CI] = 0.06 [0.03-0.09] and -0.02 [-0.05-0.02] for young and old participants, respectively, see
425 **Figure 5c**). In contrast, age was positively associated with durable compared to transient memory
426 retrieval activity in the left inferior frontal cluster and in the right superior medial frontal gyrus
427 (**Figure 5b**). Post hoc analyses revealed that in both areas, activity for durable memories was larger
428 than for transient memories in older adults, while no differences were seen in younger adults (mean
429 [CI] = -0.02 [-0.04-0.01] and 0.03 [0.01-0.05] for young and old participants, in the left inferior frontal
430 cluster –shown in **Figure 5c**; and mean [CI] = -0.03 [-0.06-0.00] and 0.05 [0.02-0.08] for young and old
431 participants, in the right superior medial frontal cluster). Age-related effects on durable memories
432 were not explained by thinner cortices in older adults as shown by post-hoc GLMs on durable
433 memory activity that included cortical thickness as an additional regressor. Cortical thickness was not
434 associated with durable memory activity ($p > 0.3$) while age remained a significant predictor of
435 durable memory activity ($p < 0.001$). See **Supplementary information** for more details. There were
436 no effects of age on encoding activity related to initial memory success. During retrieval of initial
437 memory success items, age was associated with reduced posteromedial activity and increased right
438 superior medial and right inferior frontal gyrus activity (**Supplementary Figure 4**, and **Supplementary**
439 **Table 2**).

440

441

[Insert Figure 5]

442

443 *Hippocampal analyses*

444 Four mixed effects analyses of covariance (ANCOVAs) that included hemisphere, behavioral memory
445 condition, age, and sex were performed to study whether memory success was related to
446 hippocampal activity as well as any effects of age. The ANCOVAs tested BOLD differences between
447 initial memory success and durable memory both for encoding and retrieval (Bonferroni corrected at
448 $p = 0.01$ [0.05/4]; **Figure 6**). Increased hippocampal activity was associated with initial memory
449 success both during encoding and retrieval ($F = 13.0$ [$p = 4.3e^{-4}$], $F = 29.8$ [$p = 2.1e^{-7}$], for encoding
450 and retrieval, respectively). In addition, an interaction between age and initial source memory was
451 found for retrieval ($F = 9.65$ [$p = 0.002$]), caused by lower source memory activity with higher age.
452 Both the encoding and retrieval ANCOVAs on durable memories showed trends towards increased
453 hippocampal activity for durable versus transient memories ($F = 4.8$ [$p = 0.03$], $F = 6.0$ [$p = 0.01$]
454 respectively). No age effects were found for encoding or retrieval activity of durable memories. See
455 more ANCOVAs stats in **Table 4**.

456

457 *[Insert Figure 6 about here]*458 *[Insert Table 4 about here]*

459

460 *Content-specific retrieval activity within the sensorimotor cortex*

461 It is assumed that memory retrieval involves reactivation of content-specific relevant sensory and
462 motor regions (Johnson and Rugg, 2007). To better interpret the association between sensorimotor
463 activity and durable memories, we post hoc tested for differences in retrieval activity between the
464 two encoding task instructions (“Can you eat it?” versus “Can you lift it?”). Content-specific retrieval
465 activity was revealed within the sensorimotor cortex (**Figure 7**). Content-specific activity for the eat

466 memory contrast –source for eat compared to item memory trials- was found in the left inferior
467 sensorimotor strip. This region is associated with lip and tongue representations. In contrast, the lift
468 memory contrast was associated with higher activity in the middle part of the right sensorimotor
469 strip, that grossly relates to the hand, arm and elbow representations (Meier et al., 2008; Penfield
470 and Boldrey, 1937). A post-hoc mixed-effect linear model with content-type, cluster (as within-
471 subjects) and age (as between-subjects) factors –that also included sex as a covariate of no interest-
472 did not show *age* \times *cluster* \times *content-type* effects ($F = 0.3$, $p = 0.6$) suggesting that age was not
473 associated with content-specific patterns of activity in the sensorimotor cortex. Content-specific
474 retrieval results in the sensorimotor cortex suggested a somatotopic representation of the retrieved
475 material. This strongly indicates that in the current paradigm retrieval of memories with source
476 information involved content specific reactivations.

477

478

[Insert Figure 7 about here]

479

480 4. Discussion

481

482 The results indicate that encoding and retrieval of durable memories are supported partly by
483 increased brain activity in the same brain regions that support initial memory success and partly by
484 activation of additional brain regions. In some regions, e.g. the hippocampus, durable memories
485 were supported by the same activity-based principle that governed initial memory success. Other
486 regions, however, selectively supported durable memory processing –e.g. posteromedial and frontal
487 cortices at encoding and retrieval, respectively. Importantly, while encoding activity was reduced
488 with aging, older adults' successful retrieval involved additional frontal recruitment. The implications
489 of the results are discussed.

490

491 4.1 Brain signatures of encoding of durable versus transient memories

492

493 It is known that the degree of activity in perceptual, attentional and storage brain networks during
494 the encoding of events predicts subsequent memory over shorter time intervals (e.g. (Kim, 2011)).
495 Here we showed that hippocampal and neocortical activity predicted whether an item would be
496 remembered for a long time or forgotten after being successfully recalled in a short delay test. High
497 levels of activity in these regions might reflect the interaction of incoming information with existing
498 representations (Burgess et al., 2001; Byrne et al., 2007). The relevance of hippocampal-posterior
499 cortical circuitry that involves DMN and higher order visual processing nodes, for establishing durable
500 memories is in good agreement with previous research. Hippocampal activity during encoding has
501 previously been linked to durable memories (Carr et al., 2010; Wagner et al., 2016) as well as higher
502 visuoperceptive (Wagner et al., 2016) and posteromedial (Liu et al., 2014) cortical activity.

503

504 High levels of encoding activity likely triggers initial consolidation processes involving a myriad of
505 cellular mechanisms that ultimately lead to alterations of the synaptic efficacy (Dudai et al., 2015).
506 Yet, consolidation processes do not occur homogeneously for all the encoded information. Likely,
507 some encoding events are tagged as “salient” or “relevant” and consequently undergo system
508 consolidation processes during post-encoding periods and sleep (Payne et al., 2008; Saletin et al.,
509 2011; Stickgold and Walker, 2013). Here, we show that the likelihood of an event being stabilized in
510 long-term memory increases with increased recruitment of hippocampal and selected neocortical
511 regions –including a subset of DMN nodes– during encoding. In agreement with the notion that
512 hippocampal-neocortical ensembles constitute an initial memory trace for an episode (Nadel and
513 Moscovitch, 1997; Squire, 2004), the degree of connectivity between the hippocampus and
514 neocortical areas both during encoding (Sneve et al., 2015), sleep (Hu et al., 2015; Kaplan et al., 2016)
515 and idle post-encoding periods (Tambini et al., 2010; van Kesteren et al., 2010) has been shown to
516 predict later retrieval. The results are somewhat coherent with recent system consolidation findings
517 that suggest that both the neocortex and the hippocampus are involved during and initial encoding
518 phase, but the involvement of the latter diffuses when predicting long-lasting memories (Kitamura et
519 al., 2017).

520

521 Complementarily, cortical correlates of durable memories can reflect the beneficial engagement of
522 cognitive processes. Activity in regions supporting durable memory might reflect the construction of
523 more elaborate mental scenes, by means of deeper, self-referential and/or imagery richer encoding
524 processes which are known to increase later memory performance (Craik and Lockhart, 1972;
525 Richardson, 1980; Symons and Johnson, 1997; Trelle et al., 2015). A more elaborate mental scene
526 construction (Andrews-Hanna et al., 2010; see also Hassabis and Maguire, 2007), which requires the
527 integration of new and existing information, is thought to be involved in the current encoding task
528 and might constitute a basis for selective stabilization of memories. Altogether, with longer post-

529 encoding delays, correlates of subsequent memory success seem to shift from perceptual and
530 attentional networks towards areas more involved in mnemonic processes.

531

532 **4.2 Brain signatures of retrieval of durable versus transient memories**

533

534 Durable memories were associated with higher retrieval activity in distributed frontal and insular
535 cortical regions as well as –at a trend level– the hippocampus. Higher retrieval activity associated
536 with durable memories might indicate reactivation of stronger memory traces. Hippocampal activity
537 has been shown to characterize successful retrieval over shorter time intervals (Kim, 2016, 2010;
538 Staresina et al., 2012). The present findings extend this intensity principle to durable memories which
539 coincide with the suggestion that hippocampal activity co-varies with the amount of information
540 retrieved and involves the reactivation of the memory trace (Ritchey et al., 2013; Xue et al., 2010).
541 Activity in the sensorimotor cortex was related to both initial memory success and memory durability
542 despite rarely being associated with successful memory retrieval. Here, activity in this region likely
543 represents content-specific retrieval effects. A post hoc analysis confirmed that the patterns of
544 activity within the sensorimotor strip varied according to the content of what was retrieved,
545 following the somatotopic organization (Meier et al., 2008; Penfield and Boldrey, 1937) and
546 suggesting the presence of content-specific reactivation of the material within the somatosensory
547 cortex.

548

549 *Testing effects.* The retrieval-related activity associated with durable memories could also reflect
550 testing effects. The effort and elaboration required during an initial cued retrieval could strengthen
551 memory when tested in a later, delayed retrieval (Karpicke and Roediger, 2008; Pyc and Rawson,
552 2010; Roediger and Butler, 2011). It is likely that without the short delay test, some trials categorized

553 as durable memories in the present study would have been forgotten if they had been tested only
554 after a long period of time. Thus in the short delay retrieval, BOLD signal associated with the durable
555 memory contrast might reflect testing effects and re-encoding processes that boost memory
556 durability. More left anterior insular and right medial superior frontal activity during durable memory
557 retrieval would fit with this interpretation. While activity in the anterior insula has occasionally been
558 associated with successful retrieval measures (Kikyo et al., 2002; Slotnick and Dodson, 2005;
559 Yonelinas et al., 2005), it consistently predicts subsequent memory during encoding (Addis and
560 McAndrews, 2006; Kim, 2011; Kirwan et al., 2008). Insular activity possibly reflects monitoring
561 demands and response selection processes, and its relationship with durable memories could be
562 partially understood as the beneficial effect of effortful retrieval processes on item durability. The
563 only available evidence indicated higher activity during the retrieval of durable memories in
564 posteromedial cortex and in content-specific regions, but also in the left insular cortex (Wagner et al.,
565 2016). Further studies that rate memory strength and encoding strategies on a trial-by-trial basis are
566 needed to clarify the processes supporting durable memories during the short delay retrieval.

567

568 **4.3 Age-related effects on durable memory activity**

569

570 Older adults exhibited lower left posteromedial activity during encoding of durable versus transient
571 memories in a cluster centered in the retrosplenial cortex and encompassing the neighbouring
572 posterior cingulate and the precuneus regions. The retrosplenial cortex (and adjacent PCC regions) is
573 critical for integration of external visual information and stored representations as it is strongly
574 connected both with the hippocampal formation and the visual cortex (Kobayashi and Amaral, 2007,
575 2003). Scarce evidence of age-related effects on subsequent memory activity in the retrosplenial
576 cortex is available (Oh and Jagust, 2013; Park et al., 2013) in contrast to reduced deactivations in
577 older adults in other regions of the posteromedial cortex (Maillet and Rajah, 2014; Miller et al., 2008;

578 Park et al., 2013). Yet, aging is associated with thinning of the retrosplenial cortex (Fjell et al., 2014,
579 2013), diminished white matter integrity of the fiber bundle connecting to the medial temporal lobe
580 (Sala et al., 2012; Westlye et al., 2010) and marked source memory decline (Schacter et al., 1994,
581 1991), which relies on retrosplenial activity (Staresina and Davachi, 2006). Patients with Alzheimer's
582 disease and mild cognitive impairment have been shown to have early retrosplenial hypometabolism
583 (Chételat et al., 2016; Nestor et al., 2003), which again has been related to memory performance
584 (Desgranges et al., 2002). The retrosplenial cortex also seems fundamental for memory consolidation
585 (see Vann and colleagues [2009] for a detailed review of retrosplenial function). Monkeys with
586 experimentally-induced retrosplenial lesions exhibited diminished retention of information –as well
587 as retrograde memory impairments– despite no evidence for impaired learning (Buckley and Mitchell,
588 2016) largely agreeing with the available neuropsychological evidence (Maguire, 2001). Those
589 findings are in coherence with the present observation of weaker durable memory activity at
590 encoding with increasing age. With increasing age, the retrosplenial cortex –and the adjacent PCC–
591 might become increasingly ineffective in binding information, affecting the likelihood of an
592 association being stabilized into memory.

593

594 The age-related activity reduction could also reflect the use of different encoding mechanisms. Older
595 adults are less prone to engage deep or elaborative processes, relying more on structure or saliency
596 of the encoding material (Craik, 1983; Kamp and Zimmer, 2015). During encoding, the ventral portion
597 of the posteromedial cortex is involved in a deeper and more elaborate processing of the material
598 (Daselaar et al., 2003; Schacter et al., 2007). Different engagement of cognitive processes, such as
599 visual imagery and self-referential processing, could also explain the extension of age-dependent
600 effects into the ventral portion of the precuneus (Andrews-Hanna et al., 2010). In contrast to the
601 posteromedial cortex, durable memory activity in the hippocampus was invariant to age. This finding
602 agrees with previous reports suggesting that subsequent memory effects during encoding remain

603 stable with age (Duverne et al., 2009; Park et al., 2013), even though shorter retention intervals were
604 used in that studies.

605

606 Older adults showed higher activity in the left inferior and right superior medial frontal cortices
607 during retrieval of durable memories. This may indicate that older adults engage cognitive control
608 processes to a greater extent during the retrieval of acquired source associations (i.e. retrieval effort,
609 Wang and Cabeza, 2016). Older adults could increasingly depend on these processes to boost weaker
610 memories, while younger adults would rely on more automatically-driven reinstatement processes.
611 The left inferior frontal cortex is a central region for a plethora of control mechanisms (e.g. selection
612 mechanisms) that take place during recollection (Badre and Wagner, 2007) and is sensitive to higher
613 task demands (Badre et al., 2005). The retrieval of weaker associative memories will require a more
614 effortful processing, requiring higher task demands, and as a consequence may strengthen the
615 memory binding of the retrieved information, increasing the likelihood of being correctly
616 remembered in a later test. Previous research has revealed that testing effects rely on higher activity
617 in the prefrontal cortex (Liu et al., 2014; Liu and Reder, 2016) and increased frontotemporal
618 connectivity (Wing et al., 2013). Thus, testing effects seem to facilitate later memory through
619 mechanisms that normally support memory success at encoding (Wing et al., 2013).

620

621 **4.4. General remarks**

622

623 Memory performance declined with age both when tested after a short and a long delay. This finding
624 is in agreement with the existing literature that shows marked decline on associative memory
625 performance. Yet the rate of forgetting was unrelated with age. Although system consolidation
626 processes (including sleep dependent consolidation) seem affected by age (Scullin et al., 2017; Scullin
627 and Bliwise, 2015; cf. Aly and Moscovitch, 2010) is still unclear whether older adults exhibit steeper

628 forgetting rates (Macdonald et al., 2006; Wheeler, 2000) or else, are independent of participants'
629 age (Fjell et al., 2005; Meeter et al., 2005). In the present study, either the relatively prolonged post-
630 encoding delay (\approx 90 minutes) preceding the first retrieval or testing the same material twice
631 (Wheeler, 2000) might have led to age-invariant forgetting rates.

632

633 In addition to the vertex-wise analyses, the spatial overlap comparison showed that durable memory
634 patterns of activity at encoding and at retrieval are largely unrelated to the canonical patterns
635 associated with memory success. The analysis suggests that durable memory formation does not
636 reflect a mere extension of the same intensity principle leading to initial memory success and
637 underscores the presence of additional mechanisms at encoding -and at short delay retrieval-
638 involved in the establishment of long-lasting memories. Altogether, our results concur with previous
639 studies such as in Wagner and colleagues (2016) where the authors showed that the formation of
640 durable memories is supported both by an extension of the activity-based patterns leading to
641 encoding success as well as by the presence of additional mechanisms that involve retrieval-related
642 regions.

643

644 Testing the same memories twice allowed us to define prospectively memory durability –compared
645 with studies that test half of the encoding material at each test. Yet the followed approach may
646 induce testing effects, boosting weaker memories (Wagner et al., 2016), and making it difficult to
647 interpret the retrieval results. Though the methodology also affects trial sorting at encoding, the
648 impact is limited as reliable patterns of activity were associated with durable memory encoding. The
649 main limitations of the study are inherent to the field, most importantly the correlational nature of
650 the fMRI technique as well as the lack of longitudinal information.

651 **5. Conclusions**

652

653 The present study suggests that partially independent mechanisms support durable memories and
654 initial memory success. Long-lasting memories rely on DMN and higher visual processing nodes at
655 encoding and on frontal and insular activity during retrieval –possibly, to some degree, reflecting re-
656 encoding processes. Further, older adults showed lower posteromedial activity –encompassing the
657 retrosplenial cortex as well as adjacent posterior cingulate and precuneus regions- associated with
658 encoding and higher frontal activity during retrieval of durable memories. The age results may reflect
659 an increased difficulty to integrate new information and a possibly beneficial effect of cognitive
660 control mechanisms. However, whether the latter represents a compensatory mechanism is still
661 unclear. Further multimodal studies are needed to better understand the association between the
662 encoding and retrieval mechanisms and the ongoing long-term system consolidation processes such
663 as overnight memory reactivation.

664

665

666

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668

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675

676

677

678 **7. References**

679

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- 946

947 **8. Tables**
 948

	All	Age (t [p])
Sex (female:male)	90:53	--
Age	55.6 (13.7)	--
Age range	22:78	--
MMSE	29.0(1.0)	-1.1(0.3)
Vocabulary	65.0(7.2)	2.7(0.008)*
CVLT learning	56.0(8.8)	-3.3(0.001)*
CVLT 30'	12.6(2.5)	-3.2(0.001)*
Interrest interval (days)	34.1(14.2)	-3.1(0.002)*

949 Table 1 Main demographic and neuropsychological
 950 variables.

951 *Main demographic and neuropsychological variables.*

952 *When appropriate, effects of age on each variable*

953 *(right side; GLM with age and sex as predictors).*

954 *Descriptive statistics represent \bar{x} (SD), range or*

955 *frequencies.*

Behavioral measures	Short delay retrieval \bar{x} (SD)	Age(t[p])	Long delay retrieval \bar{x} (SD)	Age(t[p])
Source memory corrected	.40(.18)	-5.8(5.0e ⁻⁸)*	.10(.08)	-4.9(2.4e ⁻⁶)*
Source memory	.51(.13)	-3.8(2.1e ⁻⁴)*	.25(.10)	0.7(0.5)
Item	.23(.08)	3.8(2.1e ⁻⁴)*	.38(.12)	-0.7(0.5)
Miss	.23(.13)	0.6(0.6)	.35(.15)	-0.3(0.76)
Wrong recollection	.10(.07)	6.6(6.1e ⁻¹⁰)*	.15(.10)	5.2(6.6e ⁻⁷)*
Correct rejections	.91(.08)	-3.9(1.3e ⁻⁴)*	.82(.14)	-4.9(2.3e ⁻⁶)*
False alarms	.09(.08)	4.1(8.4e ⁻⁵)*	.17(.14)	5.1(9.6e ⁻⁷)*
Recognition corrected	.65(.13)	-3.8(2.2e ⁻⁴)*	.45(.14)	-5.1(8.8e ⁻⁷)*
Recognition d'	2.16(0.63)	-5.1(1.3e ⁻⁶)*	1.45(0.50)	-6.4(2.5e ⁻⁹)*

956 Table 2. Behavioral measures.

957 *Main behavioral measures from the short and long delay retrievals. All measures but Recognition*
 958 *d' are expressed in proportions. Effects of age on each measure (GLM with age and sex as*
 959 *predictors). Bonferroni corrected at $p < [0.05/8] 0.006$. Recognition corrected = Item Hits – False*
 960 *alarms.*

	All \bar{x} (SD)	Age t(p)
Durable memory	.19(.08)	-1.0(0.3)
Transient memory	.31(.11)	-3.6(4.0e ⁻⁴)*
Item memory	.23(0.08)	-1.7(0.1)
Miss memory	.26(.11)	3.8(2.1e ⁻⁴)*
Durable:Initial	.39(.14)	-1.7(0.08)
Memory success		

961 Table 3. Behavioral descriptives.

962 *Main behavioral measures in relation to the experimental fMRI*

963 *conditions. All measures are in proportions. Effect of age on each*

964 *measure (right column, GLM with age and sex as predictors).*

965 Significance was considered at $p < 0.01$ (0.05/5) after Bonferroni

966 correction for the number of behavioral comparisons.

ANCOVA	Memory	Hemisphere	Age	Sex	Memory*Age
Encoding-durable memory	4.7(0.03) [°]	0.5(0.5)	0.0(0.9)	0.8(0.4)	1.9(0.2)
Retrieval-durable memory	6.1(0.01) [°]	20.9(1.05e ⁻⁵)*	9.2(0.003)*	0.2(0.6)	1.7(0.2)
Encoding-initial memory success	13.0(4.3e ⁻⁴)*	0.7(0.4)	2.9(0.09)	0.0(0.9)	0.0(0.8)
Retrieval-initial memory success	29.8(2.1e ⁻⁷)*	16.6(7.7e ⁻⁵)*	19.7(1.81e ⁻⁵)*	0.0(1.0)	9.6(0.002)*

967 Table 4. Hippocampal activity ANCOVA.

968 *Stats (F[p]) indicating differences in hippocampal activity across conditions of interest. Significance*
 969 *was considered at $p < 0.01$ ($0.05/4$) after Bonferroni correction for multiple comparisons. * and °*
 970 *symbols denote corrected and uncorrected (trend towards) significance. None of the terms not shown*
 971 *in the table exhibited significance.*

972 **9. Caption to Figures**

973

974 Figure 1. Experimental paradigm.

975 *a) Schematic of an encoding trial. The green ✓ and the red X symbols were present on the screen to*
976 *indicate which button indicated Yes and No. b) Schematic of a retrieval trial. Test Questions 1 and 2*
977 *required a Yes/No response whereas Question 3 consisted of a two-alternative forced choice task. The*
978 *trial ended if the participant responded No to either one of the two first questions. Response cues (✓,*
979 *X, eating, lifting) were also here present on the screen. c) Overview of the study design. An incidental*
980 *memory encoding task was followed by a surprise memory test after 1.5 hours later where the old*
981 *trials were randomly mixed with new items. Approximately 5 weeks after the initial encoding,*
982 *participants underwent a second surprise memory test where the old items were re-tested mixed with*
983 *new items; d) Schematic of the behavioral conditions of interest: durable memories (DM) included*
984 *those items with source memory in both, short and long interval retrievals; transient memories (TM)*
985 *included trials with correct source memory at the first, but not in the second retrieval while Item*
986 *memory (IM) was based on trials with only item memory during the first retrieval. The red-coloured*
987 *bubble can indicate either incorrect or no source memory –as the participant could also stop the trial*
988 *on the second question. Adapted from Sneve et al. (2015).*

989 Figure 2. Main memory effects of encoding activity.

990 *Parameter estimates of encoding activity. Vertex significance is displayed in clusters surviving*
991 *multiple comparison correction by FWE (vertex-wise $p < 0.01$; cluster-based $p < 0.05$). BOLD activity*
992 *during encoding associated with a) initial memory success -source versus item memory on the first*
993 *retrieval- and b) durable memories –source memory during both retrievals versus source memory*
994 *during the first but not during the second retrieval. Positive and negative significance patterns are*
995 *shown in respective red-yellow and blue-light blue scales overlaid onto semi-inflated surfaces. See*
996 **Supplementary Table 1** *for cluster stats and* **Supplementary Figure 1** *for activity patterns during*
997 *encoding associated with the different memory conditions at different correction thresholds.*

998 Figure 3. Main memory effects of retrieval activity.

999 *Parameter estimates of retrieval activity. Vertex significance is displayed in clusters surviving multiple*
1000 *comparison correction by FWE (vertex-wise $p < 0.01$; cluster-based $p < 0.05$). BOLD activity during the*
1001 *first retrieval associated with a) initial memory success -source versus item memory on the first*
1002 *retrieval, and b) durable memories -source memory during both retrievals versus source memory*
1003 *during the first but not during the second retrieval. Positive and negative significance patterns are*
1004 *shown in respective red-yellow and blue-light blue scales overlaid onto semi-inflated surfaces. See*
1005 **Supplementary Table 1** *for cluster stats and* **Supplementary Figure 2** *for activity patterns during*
1006 *retrieval associated with the different memory conditions at different correction thresholds.*

1007 Figure 4. Spatial overlapping between memory contrast maps.

1008 *Spatial overlap between contrast a) encoding and b) retrieval maps in red and blue colors,*
1009 *respectively. Spatial overlap between: initial memory success and durable memory contrast maps (left*
1010 *column); durable memory and meta-analytic memory success contrast maps (middle column) and;*
1011 *initial memory success and meta-analytic memory success contrast maps (right column). For visual*
1012 *purposes, the plots only display the spatial correlation –after z-standardization– between a random*
1013 *subsample of vertices ($n = 1000$). See full stats in section **3. Results**. MA = meta-analytic. Overlay*
1014 *between initial memory success and durable memory contrast maps (thresholded at $p < 0.01$*
1015 *uncorrected) during c) encoding and d) retrieval. The durable memory contrast is represented in*
1016 *green, the initial memory success contrast is represented in red and the overlap is represented in*
1017 *yellow.*

1018 Figure 5. Age-related differences on durable memory-associated activity.

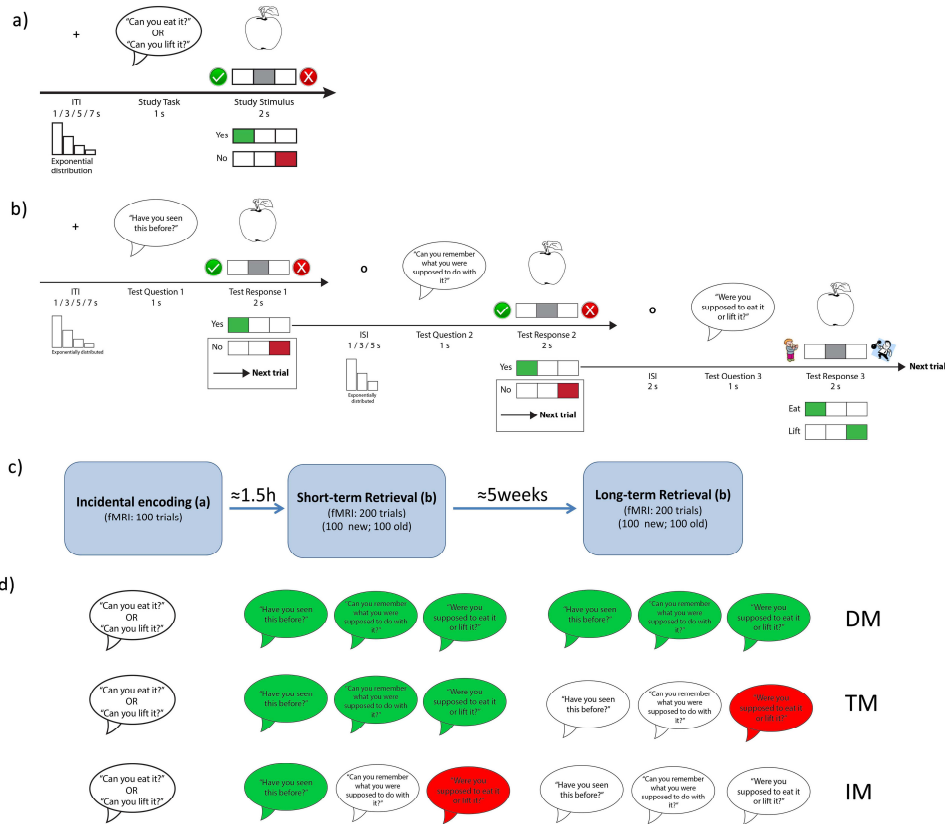
1019 *Parameter estimates of age effects on BOLD signal associated with durable memories. Vertex*
1020 *significance is displayed in clusters surviving multiple comparison correction by FWE (vertex-wise $p <$*
1021 *0.01; cluster-based $p < 0.05$). Age effects on neural activity associated with a) encoding of durable*
1022 *memories and, b) retrieval of durable memories. Positive and negative significance patterns are*
1023 *shown in red-yellow and blue-light blue scales overlaid onto semi-inflated surfaces. In c) mean signal*
1024 *change data across age is shown from clusters showing age-effects. Data from the left posteromedial*
1025 *cortex during encoding and from the left inferior frontal gyrus during retrieval is plotted in the blue*
1026 *and red scatterplots, respectively. See **Supplementary Table 2** for cluster stats.*

1027 Figure 6. Hippocampal activity on memory conditions.

1028 *Left and right hippocampus activity during the main a) encoding and b) retrieval conditions. In the*
1029 *left-side figures, activity elicited by initial memory success and item memory trials is shown while the*
1030 *right-side figures represent durable and transient memory-elicited activity. DM = durable memories;*
1031 *TM = transient memories; IMS = initial memory success; IM = item memory. * and ° symbols denote*
1032 *Bonferroni corrected ($p < 0.01$ [$0.05/4$]) and uncorrected significance ($p < 0.05$).*

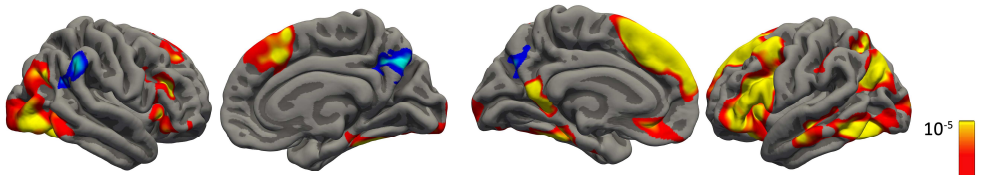
1033 Figure 7. Content-specific retrieval effects in the sensorimotor strip.

1034 *Sensorimotor regions revealing content-specific retrieval effects. Red and blue clusters represent*
1035 *regions where content-specific successful source memory retrieval activity was seen for source Eat*
1036 *and Lift questions, respectively. The red and blue bar plots represent mean signal change of activity*
1037 *between source-Eat/Lift memory trials compared to item trials. * and ° symbols denote Bonferroni*
1038 *corrected ($p < 0.01 [0.05/4]$) and uncorrected significance ($p < 0.05$). Significance patterns are shown*
1039 *in red-yellow and blue-light blue scales overlaid onto semi-inflated surfaces and represent mean*
1040 *signal change of activity between the dominant content-specific condition compared to item memory.*
1041 *See **Supplementary information** for more details.*

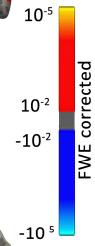
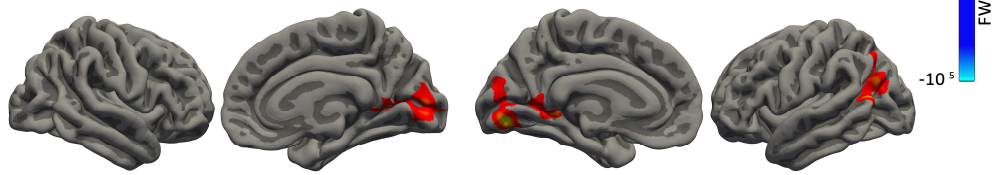


Encoding fMRI - main effects

a) Initial Memory success

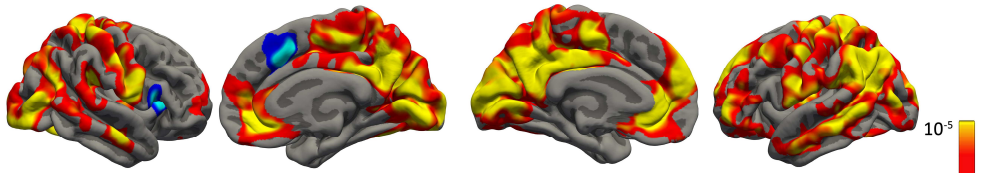


b) Durable Memory

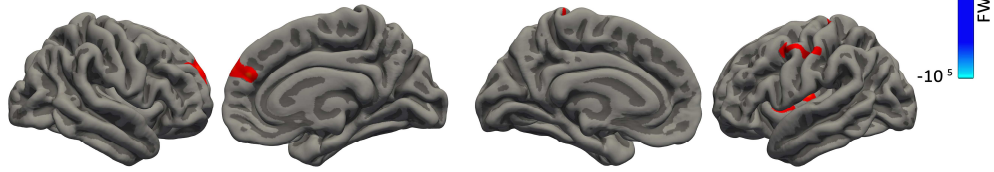


Retrieval fMRI - main effects

a) Initial Memory success

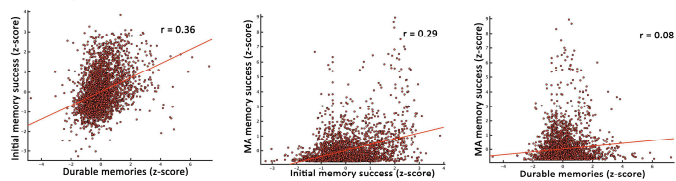


b) Durable Memory

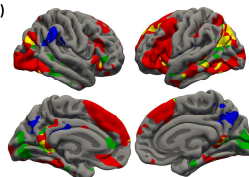


Spatial relationship between contrasts

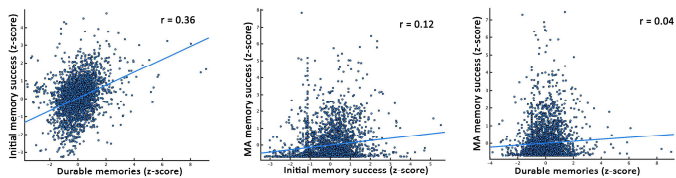
a) Encoding



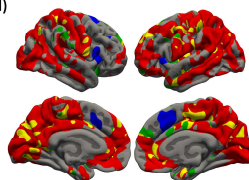
c)



b) Retrieval

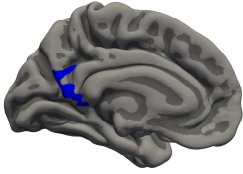


d)

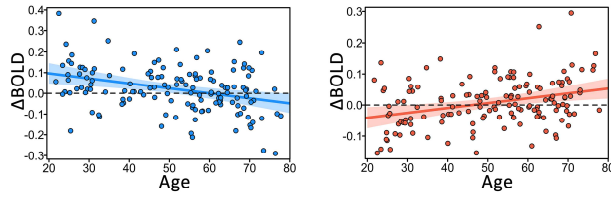


Age effects on durable memories

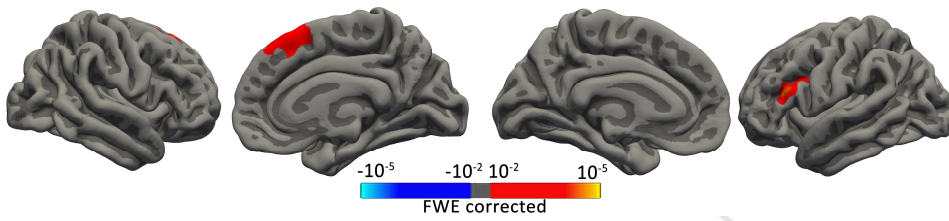
a) Encoding



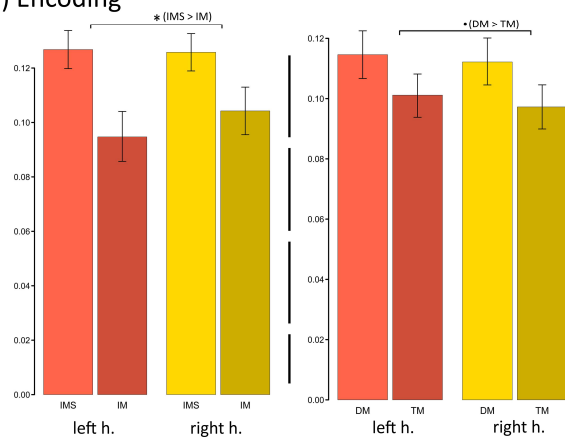
c) Scatterplots



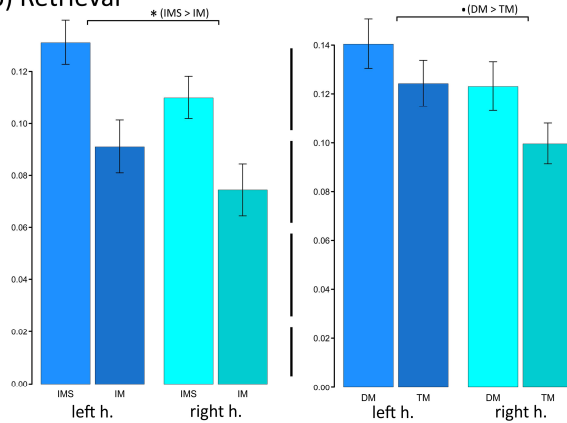
b) Retrieval

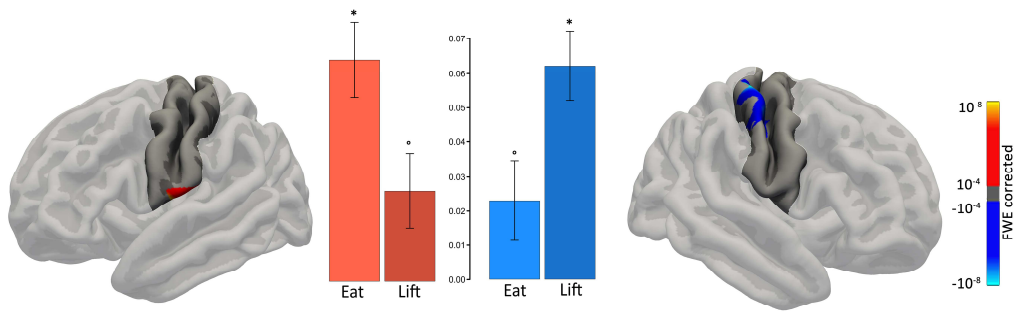


a) Encoding



b) Retrieval





1 **Neural correlates of durable memories across the adult lifespan: brain activity at encoding**
2 **and retrieval. Supplementary information.**

3
4 **1. Supplementary methods**

5
6 Participants

7 All participants were right-handed, spoke Norwegian fluently, and had normal or corrected-to-normal
8 hearing and vision. Participants were screened for neurologic or psychiatric disorders, chronic illness,
9 premature birth, learning disabilities, or current use of medicines known to affect nervous system
10 functioning. Additional inclusion criteria was defined based on neuropsychological evaluation: score ≥ 26
11 on the MiniMental State Examination (MMSE; Folstein et al., 1975), score ≥ 85 on the Wechsler
12 Abbreviated Scale of Intelligence (Wechsler, 1999), and a T-score of >30 on the California Verbal
13 Learning Test II—Alternative Version (CVLT II; Delis et al., 2000) immediate delay and long delay.

14
15 Content-specific retrieval activity in the sensorimotor cortex

16 Compared to transient memories, the short delay retrieval of durable memories was characterized by
17 higher activity in the sensorimotor cortex. A posthoc analysis was carried out to reveal whether retrieval
18 activity in the sensorimotor cortex reflected content-specific reactivation of the material. We studied
19 whether content-specific patterns of activity corresponding to the different source questions (“can you
20 eat/lift it?”) was manifested within the sensorimotor strip. We hypothesized that the patterns of activity
21 would vary according to the content of what was retrieved, following a somatotopic organization (Meier

22 et al., 2008; Penfield and Boldrey, 1937). See section **3. Results** and **Figure 7** in the main text for the
23 correspondent results.

24

25 Three behavioral conditions of interest were defined based on the short delay retrieval: 1) correct
26 source memory for items presented in association with the source *Eat* question (source-eat memory); 2)
27 correct source memory for items presented with the source *Lift* question (source-lift memory); 3) items
28 remembered without –or with incorrect- source information (item memory). Item memory trials were
29 grouped in a single condition, regardless of the accompanying source question, to improve the reliability
30 of the estimate (Wang et al., 2016). The remaining preprocessing pipeline was identical as described in
31 the main manuscript (see details in sections **2.5 MRI data preprocessing** and **2.6 fMRI analysis**). For
32 each participant, the following contrasts of parameter estimates were computed for further statistical
33 analysis: source-eat versus item memory (eat memory contrast) and source-lift versus item memory (lift
34 memory contrast). Next, individual contrasts were fed into group level ordinary least square general
35 linear model (GLM) analyses to explore the main contrast effects. The models included sex and age as
36 covariates and were restricted to the sensorimotor strip (precentral and postcentral parcellation in
37 Desikan-Killiany atlas [Desikan et al., 2006]); erosion factor = 5). Content-specific activity was defined by
38 inclusively masking vertices with significant activity for one source question ($p < 1.0e^{-4}$) and exclusively
39 masking for the alternative contrast ($p < 0.01$). Significant clusters were considered when size was >100
40 vertices. Due to inclusive/exclusive masking procedures, canonical multiple correction methods (i.e.
41 FWE/FDR correction methods) could not be easily implemented.

42

43 Morphological analysis

44 A post-hoc analysis was carried to test whether differences in structural integrity explained age
45 differences in durable memory activity. For each participant, we extracted mean cortical thickness
46 values from those regions that showed age-related effects on durable memory activity (see **Figure 5**).
47 Cortical thickness estimates from the T1-weighted images were available from the cortical
48 reconstruction (using FreeSurfer v.5.3 as described in section **2.5 MRI data preprocessing**). For each
49 cluster exhibiting age-effects, a GLM on durable memory activity was ran with age, sex and additionally,
50 regional cortical thickness.

51 1. Supplementary results

52

53 Morphological analysis

54 Age-related effects on durable memories were not explained by cortical thickness differences as shown
55 by post-hoc GLMs on durable memory activity that included cortical thickness as a regressor, in addition
56 to age and sex. Cortical thickness did not predict durable memory activity during encoding in the in the
57 left posteromedial cortex ($t = 1.0$, $p = 0.3$) nor retrieval activity in the left inferior or the right superior
58 medial frontal cortex ($t = -0.5$, $p = 0.6$; $t = 0.3$, $p = 0.7$, respectively), regions that exhibited age-related
59 effects on durable memory activity in the main analysis (**Figure 5**). Age remained associated with
60 durable memory activity in the three clusters ($t = -3.3$, $p = 0.001$; $t = 3.61$, $p = 4.2e^{-4}$; $t = 3.9$, $p = 1.6e^{-4}$,
61 respectively). Thus, the age-related effects on cortical activity were not strongly influenced by thinner
62 cortices with advancing age.

63

64 Spatial overlap between memory contrasts maps

65 The meta-analytical maps were obtained from studies that mostly included young participants. To test
66 whether different inclusion criteria regarding age affected the degree of overlap between memory
67 contrasts maps we repeated the spatial overlap analysis (see main **results** and, **Figure 4**) using initial
68 memory success and durable memory contrasts maps obtained from a participants' subsample that
69 included only young participants. The young subsample included $n = 39$ participants age <40 (age = 29.4
70 [4.9]; females = 26). Higher-level vertex-wise GLMs (controlling for age and sex) were ran to obtain
71 durable and initial memory success contrast maps specific to the young sample. Other than sample
72 selection, the spatial overlap analysis was performed as described in section **2.6 fMRI analysis**.

73 The spatial overlap between initial memory success and the meta-analytical memory maps was 0.34
74 (0.02) for encoding and 0.19 (0.02) for retrieval showing medium and small anatomical correspondence
75 with the meta-analytical results. The degree of overlap between durable memory and meta-analytical
76 memory maps was considerably lower. The overlap at encoding and at retrieval was 0.12 (0.02) and 0.06
77 (0.02) showing a small and a trivial spatial correspondence. In all the comparisons, the young subsample
78 maps exhibited a slightly higher degree of spatial overlap with the meta-analytical maps. The higher
79 degree of overlap might be explained by an increased sociodemographic similarity between samples.

80 2.- Supplementary tables

81

82

Contrast	Max sig	CWP	Size (mm ²)	MNI(x,y,z)	Area
	13.0	>4.0	10557.8	(-8.0 19.0 53.1)	lh superiorfrontal
	13.6	3.7	5475.9	(-40.8, -49.9, -9.5)	lh fusiform
	12.5	2.9	3510.1	(-42.2, -69.8, 29.9)	lh inferiorparietal
	11.0	1.6	762.0	(-5.1, -57.3, 13.3)	lh precuneus
Initial	4.3	1.4	819.0	(-16.4, -100.8, 3.9)	lh lateraloccipital
memory	-5.8	1.4	615.8	(-10.0, -67.8, 33.9)	lh precuneus
success	5.0	1.3	484.8	(-8.4, 30.8, -11.8)	lh medialorbitofrontal
during	14.1	3.5	6740.6	(41.3, -49.0, -19.3)	rh fusiform
encoding	6.9	2.2	1626.0	(8.1, 23.7, 43.5)	rh superiorfrontal
	8.8	2.0	1327.4	(43.0, 26.7, 16.5)	rh rostralmiddlefrontal
	6.6	1.9	986.6	(29.2, 22.0, -3.3)	rh lateralorbitofrontal
	-6.8	1.8	1153.8	(7.5, -69.3, 37.2)	rh precuneus
	-5.6	1.5	867.4	(55.3, -40.6, 36.2)	rh supramarginal
Durable	5.7	2.0	1248.4	(-10.7, -81.6, -4.6)	lh lingual
memories	4.5	1.9	1171.0	(-49.0, -61.1, 10.7)	lh inferiorparietal
during	4.3	1.8	731.1	(-12.0, -43.8, -1.2)	lh isthmuscingulate
encoding	4.5	2.3	1538.6	(20.1, -68.6, 2.8)	rh lingual
	15.7	>4.0	46524.8	(-8.0, -46.1, 30.3)	lh isthmuscingulate
Initial	10.3	>4.0	31602.6	(6.6, -59.7, 34.2)	rh precuneus
memory	-10.2	2.4	2969.3	(9.5, 31.3, -9.9)	rh medialorbitofrontal
success	5.2	1.6	728.2	(35.8, -11.5, -3.1)	rh insula
during	-6.3	1.6	815.7	(30.0, 23.0, 2.7)	rh lateralorbitofrontal
retrieval	-10.2	1.6	818.2	(9.1, 20.5, 41.9)	rh superiorfrontal
	8.4	1.6	855.4	(60.9, -11.0, -19.0)	rh middletemporal
Durable	3.9	1.5	481.1	(-23.6, -31.3, 55.8)	lh postcentral
memories	3.6	1.4	511.2	(-39.2, -14.7, 32.8)	lh precentral
during	4.3	1.4	395.8	(-33.9, -12.2, 10.1)	lh insula
retrieval	3.7	1.5	659.7	(9.1, 47.3, 25.4)	rh superiorfrontal

83 Supplementary Table 1. Cluster statistics of the main effects analyses.

84 *Significant clusters statistics of the main effect analyses. Four contrasts were considered:*85 *initial memory success during encoding, durable memories during encoding, initial memory*86 *success during retrieval and durable memories during retrieval. The reported clusters survived*

87 $p < 0.05$ FWE correction with a cluster defining threshold of $p < 0.01$. Cluster significance was
 88 tested through permutation testing. Max sig = maximum voxel significance; CWP = cluster-
 89 wise probability (log transformed). See **Figure 2** and **Figure 3** for corresponding visual
 90 illustrations.

91

Contrast	Max sig	CWP	Size (mm ²)	MNI(x,y,z)	Area
Initial memory success during encoding	--	--	--	--	--
Durable memories during encoding	-3.6	1.4	518.6	(-8.2, -65.8, 23.7)	lh precuneus
Initial memory success during retrieval	-5.7	1.7	1082.8	(-15.6, -49.1, 33.9)	lh precuneus
	5.5	1.6	799.2	(14.0, 23.8, 31.2)	rh superiorfrontal
	5.7	1.5	669.5	(32.9, 25.3, 9.6)	rh parstriangularis
Durable memories during retrieval	4.6	1.7	792.1	(-49.0, -24.0, 16.6)	lh parsopercularis
	3.2	1.3	522.5	(7.0, 22.5, 54.7)	rh superiorfrontal

92 Supplementary Table 2. Cluster statistics of the age effects analyses.

93 *Significant clusters statistics of the age analyses. Four contrasts were considered: initial*
 94 *memory success during encoding, durable memories during encoding; initial memory success*
 95 *during retrieval and durable memories during retrieval. The reported clusters survived $p <$*
 96 *0.05 FWE correction with a cluster defining threshold of $p < 0.01$. Cluster significance was*
 97 *tested through permutation testing. Max sig = maximum voxel significance; CWP = cluster-*
 98 *wise probability. See **Figure 5** and **Supplementary Figure 4** for corresponding visual*
 99 *illustrations.*

100

101

102

103

Behavioral measures	20	30	40	50	60	70
Sex (f:m)	15:7	11:6	19:4	19:11	20:17	6:8
Age	43.5(15.7)	34.6(14.0)	34.4(8.5)	30.9(11.6)	32.8(15.3)	28.5(16.9)
Education level^a	0:7:7:4	0:2:8:6	2:4:5:11	0:5:14:11	0:5:15:15	0:2:7:5
MMSE	26.0(2.4)	33.9(3.3)	45.5(3.1)	55.4(2.5)	65.3(3.2)	73.0(2.8)
Vocabulary	28.8(1.2)	29.2(0.8)	29.2(0.7)	29.2(0.8)	28.8(0.9)	28.3(1.2)
CVLT learning	63.2(8.0)	64.1(6.5)	62.8(9.0)	65.4(5.8)	65.4(6.3)	70.3(6.4)
CVLT 30'	59.7(8.0)	56.8(6.5)	59.3(9.0)	55.5(5.8)	53.2(6.3)	51.5(6.4)
Interrest interval (days)	13.5(2.6)	13.4(2.7)	13.5(2.0)	12.3(2.0)	11.8(2.6)	11.4(3.0)

104 Supplementary Table 3. Main demographic and neuropsychological variables parsed into age groups. ^a

105 Education levels: elementary/upper-secondary/bachelor/master or upper-tertiary (n = 135).

106

107

Short delay	20	30	40	50	60	70
Source memory	.55(.14)	.54(.10)	.58(.13)	.47(.12)	.48(.13)	.41(.12)
Item	.19(.06)	.21(.06)	.20(.08)	.26(.09)	.24(.08)	.29(.11)
Miss	.24(.11)	.23(.09)	.18(.10)	.24(.11)	.24(.11)	.24(.06)
Wrong recollection	.06(.06)	.05(.04)	.09(.07)	.13(.08)	.13(.06)	.17(.09)
Source memory corrected	.49(.15)	.48(.09)	.49(.17)	.35(.16)	.35(.15)	.24(.19)
Correct rejections	.94(.07)	.94(.03)	.91(.07)	.90(.11)	.89(.06)	.87(.07)
False alarms	.06(.07)	.05(.03)	.09(.07)	.10(.11)	.11(.06)	.13(.07)
Recognition d'	2.4(.06)	2.5(.06)	2.4(.08)	2.1(.09)	2.0(.08)	1.7(.11)
Long delay	20	30	40	50	60	70
Source memory	.24(.10)	.23(.12)	.29(.09)	.23(.08)	.26(.11)	.24(.08)
Item	.39(.11)	.41(.13)	.37(.11)	.38(.11)	.37(.12)	.38(.11)
Miss	.36(.14)	.34(.18)	.33(.13)	.37(.14)	.34(.18)	.35(.14)
Wrong recollection	.11(.06)	.10(.08)	.15(.09)	.16(.10)	.20(.10)	.19(.09)
Source memory corrected	.13(.07)	.13(.09)	.13(.09)	.07(.08)	.07(.07)	.04(.08)
Correct rejections	.89(.09)	.88(.09)	.85(.11)	.83(.12)	.77(.16)	.74(.19)
False alarms	.11(.09)	.11(.08)	.15(.11)	.17(.12)	.24(.16)	.26(.19)
Recognition d'	1.7(.11)	1.8(.13)	1.6(.11)	1.4(.11)	1.2(.12)	1.1(.11)

108 Supplementary Table 4. Main behavioural variables in the experimental task parsed into age groups.

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110 **3.- Caption to supplementary figures**

111

112

113 Supplementary Figure 1. Main encoding effects of durable memories at different cluster-defining
114 thresholds.

115 *Parameter estimates of encoding activity associated with durable memories at different cluster-defining*
116 *thresholds. Vertex significance is displayed in clusters surviving multiple comparison correction by FWE*
117 *(cluster-based $p < 0.05$) with cluster defining thresholds at a) $p < 0.001$, b) $p < 0.01$ and, c) $p < 0.05$. In d),*
118 *uncorrected $p < 0.05$ maps are additionally exhibited. Positive and negative significance patterns are*
119 *shown in red-yellow and blue-light blue scales overlaid onto semi-inflated surfaces. See **Figure 2** for*
120 *related information.*

121

122 Supplementary Figure 2. Main retrieval effects of durable memories at different cluster-defining
123 thresholds.

124 *Parameter estimates of retrieval activity associated with durable memories at different cluster-defining*
125 *thresholds. Vertex significance is displayed in clusters surviving multiple comparison correction by FWE*
126 *(cluster-based $p < 0.05$) with cluster defining thresholds at a) $p < 0.001$, b) $p < 0.01$ and, c) $p < 0.05$. In d),*
127 *uncorrected $p < 0.05$ maps are additionally exhibited. Positive and negative significance patterns are*
128 *shown in red-yellow and blue-light blue scales overlaid onto semi-inflated surfaces. See **Figure 3** for*
129 *related information.*

130

131 Supplementary Figure 3. Main effects of source memory assessed with the long delay test behavioral
132 information.

133 *Parameter estimates of encoding and retrieval activity uniquely assessed with long delay test behavioral*
134 *information. Vertex significance is displayed in clusters surviving multiple comparison correction by FWE*
135 *(vertex-wise $p < 0.01$; cluster-based $p < 0.05$). BOLD activity during a) encoding and b) retrieval*
136 *associated with source versus item memory success in the long delay test. Positive and negative*
137 *significance patterns are shown in red-yellow and blue-light blue scales overlaid onto semi-inflated*
138 *surfaces.*

139

140 Supplementary Figure 4. Age effects on initial memory success-associated retrieval activity.

141 *Parameter estimates of age effects on BOLD signal during retrieval associated with initial memory*
142 *success (source versus item memory in the short delay test regardless memory condition in the long*
143 *delay test). Vertex significance is displayed in clusters surviving multiple comparison correction by FWE*
144 *(vertex-wise $p < 0.01$; cluster-based $p < 0.05$). The scatterplots reflect each participant's mean signal*
145 *change in initial memory success condition in the significant clusters. From left to right: right insular,*
146 *right superior frontal and left posteromedial clusters. Mean regression slope and $\pm 99\%$ confidence*
147 *intervals of the mean are shown in red tones. Positive and negative relationships with age are shown in*
148 *red-yellow and blue-light blue scales overlaid onto semi-inflated surfaces.*

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The authors report no conflicts of interest.

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