

1 **Age and musical training effects on auditory short-term, long-term, and**
2 **working memory**

3
4

5 Fernández Rubio, G. ¹, Olsen, E. R. ¹, Klarlund, M. ¹, Mallon, O. ¹, Carlomagno, F. ^{1,4},
6 Vuust, P. ¹, Kringelbach, M.L. ^{1,2,3}, Brattico, E. ^{1,4}, Bonetti, L. ^{1,2,3}

7

8 ¹*Center for Music in the Brain, Department of Clinical Medicine, Aarhus University & The Royal Academy of*
9 *Music Aarhus/Aalborg, Denmark*

10 ²*Centre for Eudaimonia and Human Flourishing, University of Oxford, United Kingdom*

11 ³*Department of Psychiatry, University of Oxford, Oxford, United Kingdom*

12 ⁴*Department of Education, Psychology, Communication, University of Bari Aldo Moro, Italy*

13

14 *Corresponding author: gemmafr@clin.au.dk

15 **Abstract**

16 Cognitive aging is characterized by a gradual decline in cognitive functioning. One of the most
17 worrying deficits for older adults is a decreased capacity to memorize and remember new
18 information. In this study, we assessed auditory short-term memory (STM), long-term memory
19 (LTM), and working memory (WM) abilities of young and older adults using musical and
20 numerical tasks. Additionally, we measured musical training and tested whether this capacity
21 influences memory performance. Regarding STM, young adults scored higher than older adults
22 when making same/different judgements of rhythmic sequences, but their performance was
23 alike for melodic sequences. Higher levels of musical training were associated with enhanced
24 STM capacity for melodic sequences. In relation to LTM, young adults outperformed older
25 adults in identifying new musical sequences. Moreover, younger and older individuals with
26 high musical training outperformed those with low musical training. No group differences were
27 found in the recognition of previously memorized musical sequences. Finally, we found no
28 group differences in WM capacity, although there was a non-significant tendency for young
29 adults to outperform older adults. Overall, we found that aging differently affects several types
30 of auditory memory and that, for certain musical memory tasks, a higher level of musical
31 training provides significant advantages.

32

33 **Keywords**

34 Aging, Working memory, Short-term memory, Long-term memory, Music

35 **Introduction**

36 Normal aging is accompanied by a number of physical and psychological changes. Among
37 them, cognitive aging, or the physiological and functional age-dependent changes in the brain,
38 can become an important cause for concern in older adults.

39 Cognitive aging has been well documented in the scientific literature. Age-related declines
40 in selective ^{1, 2} and sustained ² attention are noticeable in many daily tasks (e.g., driving ³) and
41 have been linked to overall white matter atrophy ⁴, reduced interhemispheric connectivity ⁵,
42 and altered mechanisms in the frontoparietal network ^{1, 6, 7}. Deficits in executive functioning
43 also occur with advancing age, and have been described in rodents ⁸. Such deficits have been
44 reported in cognitive flexibility ^{9, 10}, planning ¹¹, and inhibitory control ⁶. In addition, age-
45 dependent deficits in processing speed can affect other cognitive domains ¹².

46 One of the most investigated age-related cognitive decays is memory. Although memory
47 functioning declines with advancing age, not all types of memory are equally affected ¹³.
48 Semantic memory, which stores factual information and general knowledge, is relatively well
49 preserved from early to late adulthood ^{14, 15}. Similarly, procedural memory, or skill knowledge,
50 is minimally affected by advancing age ^{16, 17}. Conversely, episodic memory, which is long-term
51 memory (LTM) of specific events, is highly age sensitive ^{15, 18, 19}. So is working memory (WM),
52 which is involved in the temporary storage and manipulation of information and has been
53 suggested to decline due to decreased processing speed ²⁰. Finally, short-term memory (STM),
54 or the ability to maintain information after the sensory input has been removed, also declines
55 with age ^{21, 22}. Age-related memory deficits may be due to a number of neural factors. Buckner
56 ²³ concluded that disruption of the frontostriatal systems, medial temporal lobe and associated
57 cortical networks accompanies deficits in attention, executive functioning, and long-term,
58 declarative memory. These age-related factors all contribute to memory decline and vary
59 greatly between individuals.

60 Within the field of cognitive aging, research on brain maintenance has quickly grown,
61 particularly regarding compensatory recruitment. This term refers to the increased neural
62 activation that is observed in elderly individuals when performing cognitive tasks. However,
63 age-related under-recruitment of brain areas may also occur under certain circumstances ^{24, 25}.
64 In relation to memory, bilateral recruitment of frontal areas ^{26, 27} and posterior-to-anterior shifts
65 ²⁸ in activation patterns seem to facilitate encoding of episodic memories ²⁹. Overactivation of
66 prefrontal brain regions has also been observed in patients with Alzheimer's disease during
67 object location encoding and has been associated with compensatory mechanisms ³⁰.

68 Additionally, an age-related, load-dependent increase or decrease in the activity of the
69 dorsolateral prefrontal cortex has been reported during WM tasks^{25, 31, 32}.

70 Related to compensatory recruitment, several mechanisms can mitigate cognitive decline
71 in aging^{33, 34}. In the case of memory, educational level and IQ are associated with the use of
72 effective memory strategies in older adults³⁵. Similarly, musical training has positive effects
73 on cognitive functioning in the elderly. Seinfeld et al.³⁶ found that piano training improved
74 performance on measures of visual scanning, motor ability, executive function, divided
75 attention, and inhibitory control in a group of older adults. Additionally, Hanna-Pladdy and
76 MacKay³⁷ showed that elderly musicians performed better than age-matched non-musicians
77 in nonverbal memory, naming, and executive functioning tasks.

78 In this study, we focus on differences in auditory memory functioning between young and
79 elderly adults and the effects of musical training on this cognitive domain. We wish to provide
80 further information on this broad topic by comparing the performance of two age groups on
81 several tasks that assess three types of auditory memory: STM, LTM, and WM. Some of the
82 tasks involve music, so we also study how musical training level affects memory capacity.
83 Following previous studies, we expect to observe a decline in elderly adults as compared to
84 younger adults in all the investigated memory systems (STM, LTM, and WM). Furthermore,
85 we hypothesize that the level of musical training will modulate this decline, especially in tasks
86 comprising musical stimuli.

87 **Methods**

88 **Participants**

89 The sample consisted of 77 participants (43 females, 34 males) that were divided into two age
90 groups. The young group comprised 37 participants (18 females, 19 males) aged 18 to 25 years
91 old (mean age: 21.89 ± 2.05 years). The elderly group included 40 participants (25 females, 15
92 males) aged 60 to 81 years old (mean age: 67.50 ± 5.46 years). All participants were Danish
93 and reported normal health and hearing.

94 The project was approved by the Institutional Review Board (IRB) of Aarhus University
95 (case number: DNC-IRB-2021-012). The experimental procedures complied with the
96 Declaration of Helsinki – Ethical Principles for Medical Research. Participants' informed
97 consent was obtained before starting the experiment.

98

99 **Materials and procedure**

100 We tested participants' individual STM, LTM, WM, and musical training levels in a quiet room
101 at Aarhus University Hospital (Aarhus, Denmark).

102 The Musical Ear Test ³⁸ (MET) was used to measure auditory STM abilities. The MET
103 consists of 104 trials in which participants state whether two brief musical sequences are
104 identical. The test is divided into two parts: Melody, which consists of 52 sets of melodic
105 sequences, and Rhythm, comprising 52 sets of rhythmic sequences. Due to time constraints,
106 we used a reduced version of the test consisting of 40 trials (20 sets of melodic sequences and
107 20 sets of rhythmic sequences) ^{39, 40}. Scores ranged from 0 to 20 on each part.

108 To assess auditory LTM abilities, we used an old/new auditory recognition task. During
109 the encoding part, participants were instructed to listen four times to a shortened version of
110 Johan Sebastian Bach's Prelude in C minor, BWV 847. Subsequently, during the recognition
111 part, participants were presented with brief musical sequences that were extracted from the
112 prelude ("old") and with novel musical sequences ("new") of the same length, and they were
113 asked to make an "old/new" discrimination for each trial. Scores ranged from 0 to 27 for old
114 sequences and from 0 to 54 for new sequences.

115 We also assessed domain-general WM abilities with the Digit Span (DS) and Arithmetic
116 subtests from the Working Memory index in Wechsler Adult Intelligence Scale IV ⁴¹ (WAIS
117 – IV). During the DS subtest, participants listened to sequences of numbers of increasing length
118 and were asked to repeat them in the same, inverse, or ascending order (DS Forward, DS
119 Backward, and DS Sequencing, respectively). For the Arithmetic subtest, participants

120 computed mathematical operations without external aids (e.g., paper and pencil, calculator).
121 To compute individual WM abilities, we combined the raw scores from the DS and Arithmetic
122 subtests. Scores ranged from 5 to 70.

123 Finally, formal musical training was assessed with the Goldsmiths Musical Sophistication
124 Index ⁴² (Gold – MSI) questionnaire. This self-reported measure is comprised of 39 questions
125 related to musical skills, experience, and habits. Each item is assessed on a 7-point Likert scale
126 (from “1 = Completely disagree” to “7 = Completely agree”). Here, we used the Musical
127 Training facet, which estimates an individual’s history of formal musical training. Individual
128 scores on the Musical Training facet range from 7 to 49. Here, we used a Danish version of the
129 Gold – MSI.

130

131 **Statistical analyses**

132 Descriptive statistics were estimated for all variables. A one-way multivariate analysis of
133 covariance (MANCOVA, Wilk’s Lambda [Λ], $\alpha = .05$) was performed to compare STM, LTM,
134 and WM skills between the two age groups while controlling for individual musical training
135 level. We used one independent variable with two groups (young and elderly), five dependent
136 variables (STM melody, STM rhythm, LTM old, LTM new, and WM scores) and one covariate
137 (musical training score). The effect size was calculated using partial eta squared (i.e., partial
138 η^2).

139 Afterwards, to determine the effects of the independent variable and covariate, ten
140 univariate analyses of covariance (ANCOVA) were computed individually for each of the
141 dependent variables. These were computed at $\alpha = .005$ after applying the Bonferroni correction
142 (.05 divided by the number of ANCOVAs conducted) as follow-up tests to the MANCOVA.

143

144 **Results**

145 **Descriptive statistics**

146 Descriptive statistics for the measures of STM (melody and rhythm), LTM (old and new), WM,
147 and musical training are provided in **Table 1**. Two outliers were removed from the old and new
148 variables (z-scores below -3) and four values were missing from the WM measure. **Figure 1**
149 illustrates group differences in normalized scores using raincloud plots ⁴³.

150

151

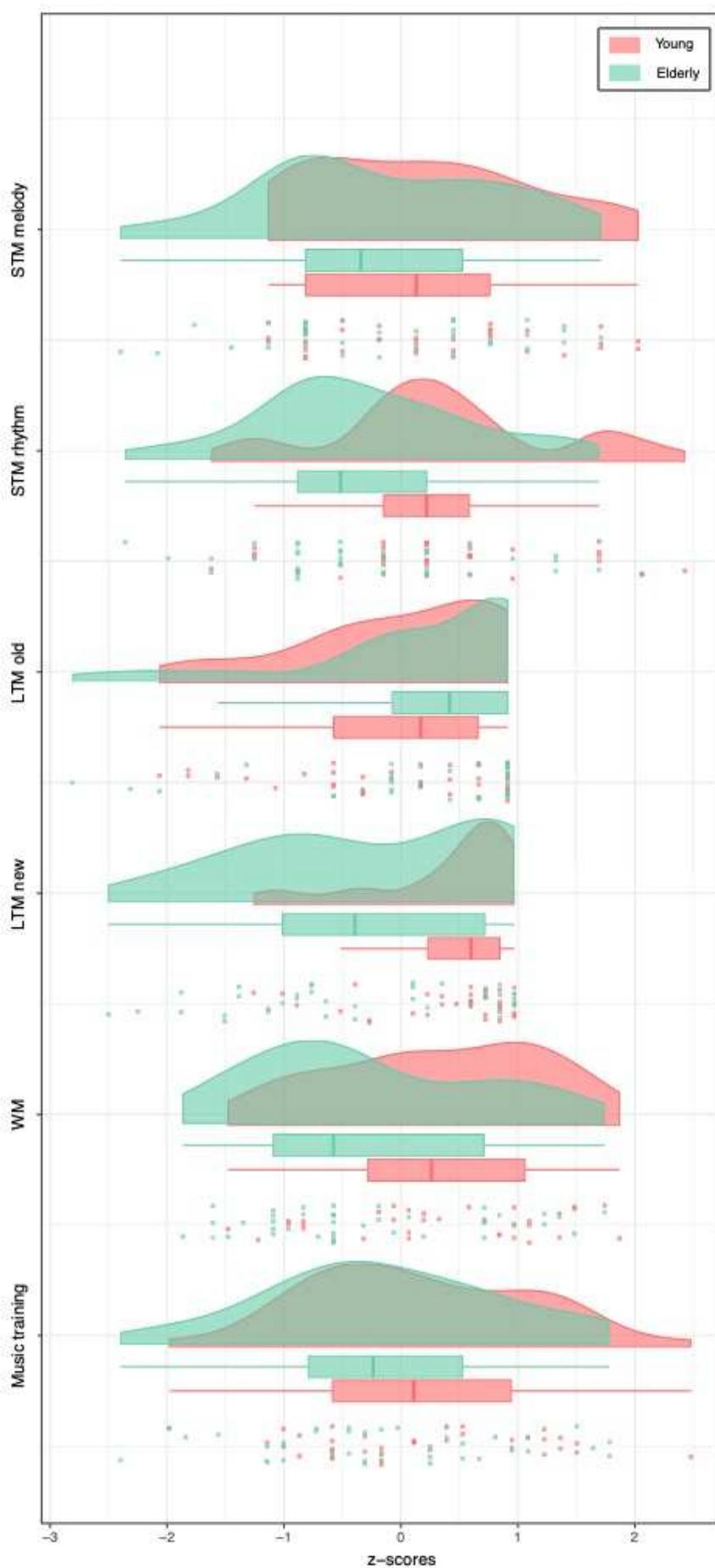
Measure	Group	
	Young (N = 37)	Elderly (N = 40)
STM melody	14.22 ± 3.02	13.00 ± 3.22
STM rhythm	14.35 ± 2.65	12.53 ± 2.5
LTM old	23.14 ± 3.56	23.5 ± 4.47
LTM new	49.19 ± 5.2	43.21 ± 9.25
WM	43.00 ± 7.15	38.26 ± 7.67
Musical training	24.30 ± 6.88	22.18 ± 7.36

152

153 **Table 1**

154 Descriptive statistics for short-term memory (STM melody and STM rhythm), long-term memory (LTM old and
155 LTM new), working memory (WM), and musical training scores as a function of group. Mean and standard
156 deviation scores are reported.

157



159 **Figure 1**

160 Raincloud plots show the overlapping distributions and normalized data points of both age groups in short-term
161 memory (STM melody and STM rhythm), long-term memory (LTM old and LTM new), working memory (WM),
162 and musical training. Boxplots show the median and interquartile (IQR, 25 – 75%) range, whiskers depict the
163 1.5*IQR from the quartile.

164

165 **Age-related differences in WM, STM, and LTM abilities**

166 In order to assess the effect of age on WM, STM and LTM abilities whilst adjusting for musical
167 training level, a one-way MANCOVA was used. Before computing the MANCOVA, we
168 confirmed there were no significant differences in musical training level between the two
169 groups ($t(75) = 1.307, p = .195$).

170 There was a statistically significant difference between the two groups on the combined
171 dependent variables after controlling for musical training level ($F(5, 64) = 4.129, p = .002$,
172 Wilks' $\Lambda = .756$, partial $\eta^2 = .24$). Follow-up ANCOVA showed statistically significant
173 differences between young and elderly participants in STM rhythm ($F(1, 74) = 10.299, p =$
174 $.001$, partial $\eta^2 = .12$) and LTM new scores ($F(1, 72) = 13.82, p < .001$, partial $\eta^2 = .16$). In
175 addition, WM approached the significance level after correction for multiple comparisons ($F(1,$
176 $70) = 7.631, p = .007$, partial $\eta^2 = .1$). On the contrary, STM melody ($F(1, 74) = 3.535, p =$
177 $.064$, partial $\eta^2 = .05$) and LTM old scores ($F(1, 72) = 0.154, p = .696$, partial $\eta^2 < .001$) were
178 not significant after controlling for musical training level.

179 There was a statistically significant effect of the covariate on the combined dependent
180 variables ($F(5, 64) = 3.858, p = .004$, Wilks' $\Lambda = .768$, partial $\eta^2 = .23$). Follow-up ANCOVA
181 showed statistically significant effects of musical training level on STM melody scores ($F(1,$
182 $74) = 17.056, p < .001$, partial $\eta^2 = .19$) and LTM new scores ($F(1, 68) = 13.46, p < .001$, partial
183 $\eta^2 = .16$), meaning that higher level of musical training was associated to higher STM melody
184 and LTM new scores. Musical training had no effect on WM ($F(1, 70) = 3.285, p = .074$, partial
185 $\eta^2 = .04$), STM rhythm ($F(1, 74) = 5.744, p = .019$, partial $\eta^2 = .07$) and LTM old scores ($F(1,$
186 $72) = 1.843, p = .17$, partial $\eta^2 = .02$).

187 **Discussion**

188 The main goal of this study was to assess the effects of age and musical training on memory
189 functioning. Our sample consisted of two age groups with matching musical training level. We
190 found significant effects of age on specific memory abilities (i.e., STM for rhythm and LTM
191 for new sequences). Additionally, we observed a positive effect of musical training level on
192 certain auditory memory tasks.

193 Concerning STM capacity, we employed a musical paradigm that comprised
194 same/different judgements of melodic and rhythmic musical sequences and confirmed that
195 STM declines with age ^{21, 22}. We found that young participants outperformed elderly
196 participants in the STM rhythm measure, but there were no significant differences in the STM
197 melody measure. These results are consistent with previous research on neural specializations
198 for rhythm and melody. Using positron emission tomography (PET), Jerde et al. ⁴⁴ showed that
199 working memory for rhythm and melody activated distinct brain networks: the cerebellum,
200 insular cortex, and cingulate gyrus for rhythmic sequences, and right frontal, parietal and
201 temporal cortices for melodic sequences. Processing of rhythm has been typically linked to
202 motor brain regions, such as the supplementary motor area, basal ganglia, and cerebellum ⁴⁵.
203 One explanation for the decreased performance we observed in the STM rhythm measure is
204 the changes in cerebellar structure that occur with advancing age ^{46, 47}. Indeed, one review
205 linked age-related differences in cerebellar volume with cognitive and motor declines ⁴⁸. This
206 distinction between rhythm and melody was also evident when examining the effect of the
207 musical training covariate. We found that musical training level had a positive effect on STM
208 for melodic sequences, but not on rhythmic sequences. Since the musical training level of both
209 groups was the same, it is reasonable that their performance was not significantly different in
210 the STM melody measure.

211 To investigate LTM capacity, we asked participants to perform a musical recognition task.
212 Once again, results differed depending on the variable analyzed: whereas young individuals
213 outperformed older individuals in identifying musical sequences that were not presented before
214 (“new”), the scores did not significantly differ when recognizing musical sequences that were
215 previously listened to (“old”). Consistent with our results, older adults have been shown
216 perform worse than young adults during free recall than recognition tasks ⁴⁹. Moreover, elderly
217 individuals exhibit increases in the number of false recognitions (i.e., remembering an event
218 that did not happen) ^{50, 51}. In terms of musical training level, we found a significant positive
219 effect of this variable on the identification of new sequences, but no effect on the recognition

220 of old sequences. This result denotes that memory recognition for musical stimuli was
221 unaffected by previous musical experience. However, the distinction of old and new musical
222 sequences required some musical skills.

223 We found no significant difference between the two age groups in WM skills. However,
224 the results from the univariate ANOVA approached the significance level after correction for
225 multiple comparisons, suggesting that young adults were close to outperform older adults. This
226 is in line with previous studies that investigated age-related decline in WM abilities ^{20, 52, 53}. In
227 this study, we employed two WM tasks that are part of the widely used WAIS – IV.
228 Performance on these tasks was previously shown to decline with age ⁵²⁻⁵⁴ and is accompanied
229 by over- or under-activation of the dorsolateral prefrontal cortex ^{25, 31, 32}. Such neural activity
230 is coherent with the compensation-related utilization of neural circuits hypothesis (CRUNCH)
231 ⁵⁵, which suggests that over-recruitment of frontal and bilateral brain regions is a compensatory
232 mechanism in older adults when task demands are low. However, as task load increases, neural
233 resources are depleted, leading to neural under-recruitment and performance decline ⁵⁶.

234 In addition to investigating differences in WM between both age groups, we also examined
235 the effect of musical training on WM ability. We found no effect of the covariate on this
236 measure. This result was expected, since the WM measure employed in this study had no
237 relation to music or musical abilities. However, previous studies have shown positive effects
238 of musical training and expertise on cognitive functioning ^{36, 37, 57} as well as relationships
239 between musical training and preferences, cognitive abilities, and neuroplasticity ⁵⁸⁻⁶⁵, so it
240 would be interesting to investigate this effect with the current WM measure in a sample of
241 musicians and non-musicians.

242 Overall, our results indicate that (1) age has an effect on memory abilities, (2) not all
243 memory types are equally affected by aging, and (3) musical training level has a positive effect
244 on specific memory and musical skills. Furthermore, we found specific effects of aging on
245 STM capacity for rhythmic sequences, but not for melodic sequences, and on LTM ability for
246 identifying new sequences, but not for recognizing old sequences. Following previous studies
247 on the spatiotemporal dynamics of memory ⁶⁶⁻⁶⁹, our future research will focus on correlating
248 these differences in memory capacity to the patterns of brain activity and connectivity during
249 short-term auditory memory recognition.

250

251 **Acknowledgements**

252 We thank the Society for Education and Music Psychology (SEMPRE) for granting LB the
253 SEMPRE's 50th Anniversary Awards Scheme which was fundamental for realising this
254 study.

255 The Center for Music in the Brain (MIB) is funded by the Danish National Research
256 Foundation (project number DNRF117).

257 LB is supported by Carlsberg Foundation (CF20-0239), Center for Music in the Brain,
258 Linacre College of the University of Oxford, and Society for Education and Music
259 Psychology (SEMPRE's 50th Anniversary Awards Scheme).

260 MLK is supported by Center for Music in the Brain, funded by the Danish National
261 Research Foundation (DNRF117), and Centre for Eudaimonia and Human Flourishing
262 funded by the Pettit and Carlsberg Foundations.

263 We thank Francesco De Benedetto for his assistance in the data collection.

264

265 **Data availability**

266

267 The anonymized data from the experiment will be made available upon reasonable request.

268 **Author contributions**

269

270 LB and EB conceived the hypotheses and designed the study. GFR, FC, ERO, OM, MK,
271 and LB collected the experimental data. GFR and LB performed statistical analyses. GFR
272 wrote the first draft of the manuscript. GFR and LB prepared the figures. PV, MLK, EB,
273 and LB secured the fundings. MLK, PV, EB, and LB provided essential help to interpret and
274 frame the results within the psychological and neuroscientific literature. All authors
275 contributed to and approved the final version of the manuscript.

276 **References**

- 277 1. Geerligs, L., Saliasi, E., Maurits, N.M., Renken, R.J., & Lorist, M.M. Brain mechanisms
278 underlying the effects of aging on different aspects of selective attention. *NeuroImage*
279 **91**, 52-62; (2014).
- 280 2. McAvinue, L.P., Habekost, T., Johnson, K.A., Kyllingsbæk, S., Vangkilde, S., Bundesen,
281 C., & Robertson, I.H. Sustained attention, attentional selectivity, and attentional capacity
282 across the lifespan. *Attention, Perception, & Psychophysics* **74**, 1570-1582; (2012).
- 283 3. Parasuraman, R., & Nestor, P.G. Attention and driving skills in aging and Alzheimer's
284 disease. *Human Factors* **33**, 539-557; (1991).
- 285 4. Gunning-Dixon, F.M., Brickman, A.M., Cheng, J.C., & Alexopoulos, G.S. Aging of
286 cerebral white matter: a review of MRI findings. *International Journal of Geriatric
287 Psychiatry: A journal of the psychiatry of late life and allied sciences* **24**, 109-117;
288 (2009).
- 289 5. Zhao, J., Manza, P., Wiers, C., Song, H., Zhuang, P., Gu, J., Shi, Y., Wang, G.-J., & He,
290 D. Age-related decreases in interhemispheric resting-state functional connectivity and
291 their relationship with executive function. *Frontiers in Aging Neuroscience* **12**, 20;
292 (2020).
- 293 6. Chao, L., & Knight, R. Prefrontal deficits in attention and inhibitory control with aging.
294 *Cerebral Cortex (New York, NY: 1991)* **7**, 63-69; (1997).
- 295 7. Madden, D.J., Spaniol, J., Whiting, W.L., Bucur, B., Provenzale, J.M., Cabeza, R., White,
296 L.E., & Huettel, S.A. Adult age differences in the functional neuroanatomy of visual
297 attention: a combined fMRI and DTI study. *Neurobiology of Aging* **28**, 459-476; (2007).
- 298 8. Bizon, J.L., Foster, T.C., Alexander, G.E., & Glisky, E.L. Characterizing cognitive aging
299 of working memory and executive function in animal models. *Frontiers in Aging
300 Neuroscience* **4**, 19; (2012).
- 301 9. Wecker, N.S., Kramer, J.H., Hallam, B.J., & Delis, D.C. Mental flexibility: age effects on
302 switching. *Neuropsychology* **19**, 345; (2005).
- 303 10. Oosterman, J.M., Vogels, R.L., van Harten, B., Gouw, A.A., Poggesi, A., Scheltens, P.,
304 Kessels, R.P., & Scherder, E.J. Assessing mental flexibility: neuroanatomical and
305 neuropsychological correlates of the Trail Making Test in elderly people. *The clinical
306 neuropsychologist* **24**, 203-219; (2010).
- 307 11. Sorel, O., & Pennequin, V. Aging of the planning process: The role of executive
308 functioning. *Brain and Cognition* **66**, 196-201; (2008).

309 12. Salthouse, T.A. Aging and measures of processing speed. *Biological Psychology* **54**, 35-
310 54; (2000).

311 13. Grady, C.L., & Craik, F.I. Changes in memory processing with age. *Current Opinion in*
312 *Neurobiology* **10**, 224-231; (2000).

313 14. Bäckman, L., & Nilsson, L.-G. Semantic memory functioning across the adult life span.
314 *European Psychologist* **1**, 27; (1996).

315 15. Rönnlund, M., Nyberg, L., Bäckman, L., & Nilsson, L.-G. Stability, growth, and decline
316 in adult life span development of declarative memory: cross-sectional and longitudinal
317 data from a population-based study. *Psychology and Aging* **20**, 3; (2005).

318 16. Korman, M., Dagan, Y., & Karni, A. Nap it or leave it in the elderly: a nap after practice
319 relaxes age-related limitations in procedural memory consolidation. *Neuroscience Letters*
320 **606**, 173-176; (2015).

321 17. Churchill, J.D., Stanis, J.J., Press, C., Kushelev, M., & Greenough, W.T. Is procedural
322 memory relatively spared from age effects? *Neurobiology of Aging* **24**, 883-92;
323 10.1016/s0197-4580(02)00194-x (2003).

324 18. Nyberg, L., Maitland, S.B., Rönnlund, M., Bäckman, L., Dixon, R.A., Wahlin, Å., &
325 Nilsson, L.-G. Selective adult age differences in an age-invariant multifactor model of
326 declarative memory. *Psychology and Aging* **18**, 149; (2003).

327 19. Nyberg, L., Bäckman, L., Erngrund, K., Olofsson, U., & Nilsson, L.-G. Age differences
328 in episodic memory, semantic memory, and priming: Relationships to demographic,
329 intellectual, and biological factors. *The Journals of Gerontology Series B: Psychological*
330 *Sciences and Social Sciences* **51**, P234-P240; (1996).

331 20. Salthouse, T.A. The aging of working memory. *Neuropsychology* **8**, 535; (1994).

332 21. Naveh-Benjamin, M., Cowan, N., Kilb, A., & Chen, Z. Age-related differences in
333 immediate serial recall: Dissociating chunk formation and capacity. *Memory and*
334 *Cognition* **35**, 724-737; (2007).

335 22. Nyberg, L., Lövdén, M., Riklund, K., Lindenberger, U., & Bäckman, L. Memory aging
336 and brain maintenance. *Trends in Cognitive Sciences* **16**, 292-305; (2012).

337 23. Buckner, R.L. Memory and executive function in aging and AD: multiple factors that
338 cause decline and reserve factors that compensate. *Neuron* **44**, 195-208; (2004).

339 24. Logan, J.M., Sanders, A.L., Snyder, A.Z., Morris, J.C., & Buckner, R.L. Under-
340 recruitment and nonselective recruitment: dissociable neural mechanisms associated with
341 aging. *Neuron* **33**, 827-840; (2002).

342 25. Cappell, K.A., Gmeindl, L., & Reuter-Lorenz, P.A. Age differences in prefrontal
343 recruitment during verbal working memory maintenance depend on memory load. *Cortex*
344 **46**, 462-473; (2010).

345 26. Cabeza, R., Anderson, N.D., Locantore, J.K., & McIntosh, A.R. Aging gracefully:
346 compensatory brain activity in high-performing older adults. *NeuroImage* **17**, 1394-1402;
347 (2002).

348 27. Gutchess, A.H., Welsh, R.C., Hedden, T., Bangert, A., Minear, M., Liu, L.L., & Park,
349 D.C. Aging and the neural correlates of successful picture encoding: frontal activations
350 compensate for decreased medial-temporal activity. *Journal of cognitive neuroscience*
351 **17**, 84-96; (2005).

352 28. Davis, S.W., Dennis, N.A., Daselaar, S.M., Fleck, M.S., & Cabeza, R. Que PASA? The
353 posterior-anterior shift in aging. *Cerebral Cortex* **18**, 1201-1209; (2008).

354 29. Craik, F.I., & Rose, N.S. Memory encoding and aging: A neurocognitive perspective.
355 *Neuroscience & Biobehavioral Reviews* **36**, 1729-1739; (2012).

356 30. Gould, R., Arroyo, B., Brown, R., Owen, A., Bullmore, E., & Howard, R. Brain
357 mechanisms of successful compensation during learning in Alzheimer disease. *Neurology*
358 **67**, 1011-1017; (2006).

359 31. Reuter-Lorenz, P.A., Jonides, J., Smith, E.E., Hartley, A., Miller, A., Marshuetz, C., &
360 Koepp, R.A. Age differences in the frontal lateralization of verbal and spatial working
361 memory revealed by PET. *Journal of cognitive neuroscience* **12**, 174-187; (2000).

362 32. Rypma, B., & D'Esposito, M. Isolating the neural mechanisms of age-related changes in
363 human working memory. *Nature Neuroscience* **3**, 509-515; (2000).

364 33. Stern, Y. What is cognitive reserve? Theory and research application of the reserve
365 concept. *Journal of the International Neuropsychological Society* **8**, 448-460; (2002).

366 34. Stern, Y. The concept of cognitive reserve: a catalyst for research. *Journal of Clinical and*
367 *Experimental Neuropsychology* **25**, 589-593; (2003).

368 35. Frankenmolen, N.L., Fasotti, L., Kessels, R.P., & Oosterman, J.M. The influence of
369 cognitive reserve and age on the use of memory strategies. *Experimental Aging Research*
370 **44**, 117-134; (2018).

371 36. Seinfeld, S., Figueroa, H., Ortiz-Gil, J., & Sanchez-Vives, M.V. Effects of music learning
372 and piano practice on cognitive function, mood and quality of life in older adults.
373 *Frontiers in Psychology* **4**, 810; (2013).

374 37. Hanna-Pladdy, B., & MacKay, A. The relation between instrumental musical activity and
375 cognitive aging. *Neuropsychology* **25**, 378; (2011).

376 38. Wallentin, M., Nielsen, A.H., Friis-Olivarius, M., Vuust, C., & Vuust, P. The Musical Ear
377 Test, a new reliable test for measuring musical competence. *Learning and Individual*
378 *Differences* **20**, 188-196; (2010).

379 39. Harrison, P.M., Musil, J.J., & Müllensiefen, D. Modelling melodic discrimination tests:
380 Descriptive and explanatory approaches. *Journal of New Music Research* **45**, 265-280;
381 (2016).

382 40. Harrison, P., Collins, T., & Müllensiefen, D. Applying modern psychometric techniques
383 to melodic discrimination testing: Item response theory, computerised adaptive testing,
384 and automatic item generation. *Scientific Reports* **7**, 1-18; (2017).

385 41. Wechsler, D. Subtest Administration and Scoring. WAIS-IV: Administration and Scoring
386 Manual. *San Antonio, TX: The Psychological Corporation*, 87-93; (2009).

387 42. Müllensiefen, D., Gingras, B., Musil, J., & Stewart, L. Measuring the facets of musicality:
388 The Goldsmiths Musical Sophistication Index (Gold-MSI). *Personality and Individual*
389 *Differences* **60**, S35; (2014).

390 43. Allen, M., Poggiali, D., Whitaker, K., Marshall, T.R., & Kievit, R.A. Raincloud plots: a
391 multi-platform tool for robust data visualization. *Wellcome open research* **4**, (2019).

392 44. Jerde, T.A., Childs, S.K., Handy, S.T., Nagode, J.C., & Pardo, J.V. Dissociable systems
393 of working memory for rhythm and melody. *NeuroImage* **57**, 1572-1579; (2011).

394 45. Kotz, S.A., Ravignani, A., & Fitch, W.T. The evolution of rhythm processing. *Trends in*
395 *Cognitive Sciences* **22**, 896-910; (2018).

396 46. Han, S., An, Y., Carass, A., Prince, J.L., & Resnick, S.M. Longitudinal analysis of
397 regional cerebellum volumes during normal aging. *NeuroImage* **220**, 117062; (2020).

398 47. Woodruff-Pak, D.S., Foy, M.R., Akopian, G.G., Lee, K.H., Zach, J., Nguyen, K.P.T.,
399 Comalli, D.M., Kennard, J.A., Agelan, A., & Thompson, R.F. Differential effects and
400 rates of normal aging in cerebellum and hippocampus. *Proceedings of the National*
401 *Academy of Sciences* **107**, 1624-1629; (2010).

402 48. Bernard, J.A., & Seidler, R.D. Moving forward: age effects on the cerebellum underlie
403 cognitive and motor declines. *Neuroscience & Biobehavioral Reviews* **42**, 193-207;
404 (2014).

405 49. Rhodes, S., Greene, N.R., & Naveh-Benjamin, M. Age-related differences in recall and
406 recognition: A meta-analysis. *Psychonomic Bulletin & Review* **26**, 1529-1547; (2019).

407 50. Schacter, D.L., Koutstaal, W., & Norman, K.A. False memories and aging. *Trends in*
408 *Cognitive Sciences* **1**, 229-236; (1997).

409 51. Gutchess, A.H., Hebrank, A., Sutton, B.P., Leshikar, E., Chee, M.W., Tan, J.C., Goh,
410 J.O., & Park, D.C. Contextual interference in recognition memory with age. *NeuroImage*
411 **35**, 1338-1347; (2007).

412 52. Grégoire, J., & Van der Linden, M. Effect of age on forward and backward digit spans.
413 *Aging, neuropsychology, and cognition* **4**, 140-149; (1997).

414 53. Choi, H.J., Lee, D.Y., Seo, E.H., Jo, M.K., Sohn, B.K., Choe, Y.M., Byun, M.S., Kim,
415 J.W., Kim, S.G., & Yoon, J.C. A normative study of the digit span in an educationally
416 diverse elderly population. *Psychiatry Investigation* **11**, 39; (2014).

417 54. Rozencwajg, P., Schaeffer, O., & Lefebvre, V. Arithmetic and aging: Impact of
418 quantitative knowledge and processing speed. *Learning and Individual Differences* **20**,
419 452-458; (2010).

420 55. Reuter-Lorenz, P.A., & Cappell, K.A. Neurocognitive aging and the compensation
421 hypothesis. *Current directions in psychological science* **17**, 177-182; (2008).

422 56. Schneider-Garces, N.J., Gordon, B.A., Brumback-Peltz, C.R., Shin, E., Lee, Y., Sutton,
423 B.P., Maclin, E.L., Gratton, G., & Fabiani, M. Span, CRUNCH, and beyond: working
424 memory capacity and the aging brain. *Journal of cognitive neuroscience* **22**, 655-669;
425 (2010).

426 57. Criscuolo, A., Bonetti, L., Särkämö, T., Kliuchko, M., & Brattico, E. On the association
427 between musical training, intelligence and executive functions in adulthood. *Frontiers in*
428 *Psychology* **10**, 1704; (2019).

429 58. Bonetti, L., Haumann, N., Vuust, P., Kliuchko, M., & Brattico, E. Risk of depression
430 enhances auditory Pitch discrimination in the brain as indexed by the mismatch negativity.
431 *Clinical Neurophysiology* **128**, 1923-1936; (2017).

432 59. Bonetti, L., Haumann, N., Brattico, E., Kliuchko, M., Vuust, P., Särkämö, T., & Näätänen,
433 R. Auditory sensory memory and working memory skills: Association between frontal
434 MMN and performance scores. *Brain Research* **1700**, 86-98; (2018).

435 60. Bonetti, L., & Costa, M. Musical mode and visual-spatial cross-modal associations in
436 infants and adults. *Musicae Scientiae* **23**, 50-68; (2019).

437 61. Bonetti, L., & Costa, M. Intelligence and musical mode preference. *Empirical Studies of*
438 *the Arts* **34**, 160-176; (2016).

439 62. Pando-Naude, V., Patyczek, A., Bonetti, L., & Vuust, P. An ALE meta-analytic review
440 of top-down and bottom-up processing of music in the brain. *Scientific Reports* **11**, 1-15;
441 (2021).

442 63. Criscuolo, A., Pando-Naude, V., Bonetti, L., Vuust, P., & Brattico, E. An ALE meta-
443 analytic review of musical expertise. *Scientific Reports* **12**, 1-17; (2022).

444 64. Iorio, C., Brattico, E., Munk Larsen, F., Vuust, P., & Bonetti, L. The effect of mental
445 practice on music memorization. *Psychology of Music* **50**, 230-244; (2022).

446 65. Bonetti, L., Brattico, E., Vuust, P., Kliuchko, M., & Saarikallio, S. Intelligence and music:
447 Lower intelligent quotient is associated with higher use of music for experiencing strong
448 sensations. *Empirical Studies of the Arts* **39**, 194-215; (2021).

449 66. Bonetti, L., Brattico, E., Carlomagno, F., Donati, G., Cabral, J., Haumann, N.T., Deco,
450 G., Vuust, P., & Kringelbach, M.L. Rapid encoding of musical tones discovered in whole-
451 brain connectivity. *NeuroImage* **245**, 118735; 10.1016/j.neuroimage.2021.118735
452 (2021).

453 67. Bonetti, L., Brattico, E., Carlomagno, F., Cabral, J., Stevner, A., Deco, G., Whybrow,
454 P.C., Pearce, M., Pantazis, D., & Vuust, P. Spatiotemporal brain dynamics during
455 recognition of the music of Johann Sebastian Bach. *bioRxiv*, (2020).

456 68. Fernández Rubio, G., Brattico, E., Kotz, S.A., Kringelbach, M.L., Vuust, P., & Bonetti,
457 L. The spatiotemporal dynamics of recognition memory for complex versus simple
458 auditory sequences. *bioRxiv*, 2022.05.15.492038; 10.1101/2022.05.15.492038 (2022).

459 69. Fernández Rubio, G., Carlomagno, F., Vuust, P., Kringelbach, M.L., & Bonetti, L.
460 Associations between abstract working memory abilities and brain activity underlying
461 long-term recognition of auditory sequences. *bioRxiv*, (2022).

462

463 **Competing interests' statement**

464

465 The authors declare no competing interests.