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1 Age-related decline in visuo-spatial working memory is reflected by dorsolateral prefrontal
2 activation and cognitive capabilities

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14 oxygenation

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22

23 **Abstract**

24 **Introduction**

25 Visuo-spatial working memory (VSWM) performances undergo a decline throughout ageing
26 and are affected by the space in which the task is performed (reaching or navigational).
27 Cerebral oxygenation and cognitive capabilities could explain this decline. We assessed the
28 effects of age on cerebral oxygenation of the dorsolateral prefrontal cortex (dlPFC) in
29 VSWM tasks in reaching and navigational space. We also assessed cognitive correlates of
30 VSWM performance in each space.

31 **Method**

32 Thirty-one (31) young adults (YA) and 24 healthy older adults (OA) performed a battery of
33 neuropsychological tests and the electronic Corsi Block-tapping Test in reaching space (e-
34 CBT) and in navigational space on the "Virtual Carpet" (VWCT). Participants were asked to
35 memorize and recall a sequential pathway, progressively increasing from 2 to 9 blocks. Their
36 span score reflected VSWM performance. The dlPFC oxygenation (oxyhaemoglobin: ΔO_2Hb
37 and deoxyhaemoglobin: ΔHHb) was measured by using functional NIRS (fNIRS) during the
38 encoding of the sequential pathway in both tasks.

39 **Results**

40 YA had higher span scores than OA in both spaces. We identified a significantly stronger
41 decrease of ΔHHb in YA compared to OA during encoding in VWCT. OA also exhibited
42 significantly lower cerebral oxygenation in VWCT compared to e-CBT. A decrease of ΔHHb
43 was also associated with a better performance in VWCT. Finally, we identified an
44 association of mental rotation and executive functions with VSWM performance in both
45 tasks.

46 **Conclusion**

47 VSWM performance and cerebral oxygenation during encoding are impacted by ageing.
48 Space in which the task was performed was associated with different cognitive functions and
49 revealed differences in cerebral oxygenation.

50

51 **Keywords:**

52 Functional near-infrared spectroscopy, prefrontal cortex, ageing, visuo-spatial working
53 memory, spatial navigation, cognition

54

55 **List of abbreviations:**

56 VSWM, visuo-spatial working memory; CBT, Corsi Block Tapping-test; e-CBT, electronic
57 Corsi Block Tapping-test; VWCT, Virtual Walking Corsi Task; dlPFC, dorsolateral prefrontal
58 cortex; fNIRS, functional Near-Infrared Spectroscopy; ΔO_2Hb , oxyhaemoglobin; ΔHHb ,
59 deoxyhaemoglobin; EF, executive functions; OA, Older adults; YA, Young adults;
60 CRUNCH, Compensation-related Utilization of Neural Circuits Hypothesis; WM, Working
61 Memory.

62 *1. Introduction*

63

64 Ageing is associated with spatial memory decline, including visuo-spatial working memory
65 (VSWM) (Iachini, Iavarone, Senese, Ruotolo, & Ruggiero, 2009). VSWM seems to be one of
66 the major cognitive processes involved in spatial navigation and route learning (Meneghetti,
67 Borella, Carbone, Martinelli, & De Beni, 2016; Lithfous et al., 2013). VSWM could be
68 involved in maintaining spatial information during navigation, recall of previously visited
69 locations and cognitive mapping of the environment (Lithfous et al., 2013).

70 The Corsi Block Tapping-Test (CBT) (Corsi, 1972) is one of the most widely used clinical
71 tests to assess VSWM in reaching space and has also been developed on a larger scale for
72 performance in navigational space: the Walking Corsi Test (Piccardi et al., 2008). This test
73 has been further improved by computer control of both a table electronic Corsi Block Test and
74 a computer-controlled set of light and tactile tiles: the “Magic Carpet”. These have been used
75 for navigational deficit studies in several pathologies in adult patients (Perrochon, Kemoun,
76 Dugué & Berthoz, 2014), and children (age 6 to adulthood) (Belmonti, Berthoz, Cioni, Fiori
77 & Guzetta, 2015). Studies in ageing have also shown that young adults (YA) outperformed
78 older adults (OA) in VSWM performances in different spaces (reaching vs. navigational)
79 (Piccardi, Iaria, Bianchini, Zompanti, & Guariglia, 2011; Piccardi et al., 2013; Perrochon,
80 Kemoun, Dugué, & Berthoz, 2014; Perrochon et al., 2018).

81

82 Many authors have shown that VSWM performances in reaching and navigation spaces are
83 different, leading to the existence of two distinct VSWM systems (Piccardi et al., 2008, 2013,
84 2014; Nori et al., 2015). Space seems to impact OA VSWM performances, since
85 performances in reaching space appeared to be superior to those in navigational space
86 (Perrochon et al., 2014; Piccardi et al., 2011). These differences could be based on the fact

87 that CBT in navigational space may require more and richer cognitive processes than in
88 reaching space (storage of spatial information), and thus may be more suited for the measure
89 of a spatial memory closer to ecological conditions (Piccardi et al., 2008, 2013, 2014; Nori et
90 al., 2015). Indeed, spatial cognition is associated with various perceptual and cognitive
91 processes, such as executive functions (EF) (Berthoz & Viaud-Delmon, 1999; Wolbers &
92 Hegarty, 2010; Lithfous et al., 2013; Taillade et al., 2013; Korthauer, Nowak, Frahm, &
93 Driscoll, 2017). EF may allow individuals to maintain their goal, plan and select the
94 appropriate strategies, manage their performance and flexibly adapt their mental state to
95 environmental properties by maintaining relevant information and inhibiting irrelevant ones (
96 West, 1996). Anatomically, EF are known to strongly rely on the frontal lobe and especially
97 the dorsolateral prefrontal cortex (dlPFC) (Baddeley, 1998; Curtis & D'Esposito, 2003). Also,
98 the involvement of VSWM and EF can be reflected in increased cerebral blood flow in the
99 dlPFC during several spatial cognition tasks (Lithfous et al., 2013; Maguire et al., 1998).
100 More precisely for VSWM, a fMRI study has highlighted dlPFC activation in a young
101 population during the encoding of sequences in reaching space (Toepfer et al., 2010). In
102 another fMRI study comparing brain activation of a young population in reaching and in
103 navigational space, authors found that the dlPFC was specifically associated with navigational
104 space (Nemmi et al., 2013). Although this theory still requires investigation, Nemmi et al.
105 have hypothesized that the two VSWM systems depending on spaces (Piccardi et al., 2008,
106 2013, 2014; Nori et al., 2015) may be supported by distinct neural basis (Nemmi et al., 2013).

107

108 Global cognition and EF are declining with age due to impairment in the functional and
109 structural integrity of the brain (Craik & Salthouse, 2011; Raz, 2000; Park, 2000; West,
110 1996). Specifically, the dlPFC exhibits major shrinkage with age, which could explain the
111 age-related EF decline in normal aging (Raz, 2000; West, 1996). OA compensate for these

112 age-related brain changes by using new strategies and by recruiting new neural structures, as
113 suggested by the Compensation-related Utilization of Neural Circuits Hypothesis (CRUNCH
114 model), a model of neurocognitive ageing (Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz &
115 Lustig, 2005). It appears that OA show different patterns of brain activation than YA. The
116 first pattern is an age-related overactivation occurring at easy and intermediate levels (low
117 cognitive load). As OA reach their maximal load capacity sooner than YA, they recruit more
118 neural circuits involved in the task, a compensatory mechanisms that allows age-equivalent
119 performances. These are interpreted as strategic or neural adjustments to compensate
120 processing inefficiency, local or elsewhere. Another pattern seems to be frequently observed
121 at high levels of difficulty (high cognitive load): we detect an under-activation of the required
122 brain areas in OA compared to YA, which leads to poorer cognitive performances.
123 Compensatory mechanisms for the functional deficiency in the processing mediated by the
124 areas are no longer effective at these levels of cognitive load, as a result of reaching a
125 resource ceiling. This under-activation might reflect poor strategy uses and the subsequent
126 recruitment of brain structures which are inadequate for the task (Logan, Sanders, Snyder,
127 Morris, & Buckner, 2002; Reuter-Lorenz & Lustig, 2005), and therefore may explain low
128 performances in OA. Rather than simply occurring at a high cognitive load, Schneider-
129 Garces, Gordon, Brumback-Peltz & Shin (2010) found evidence that this under-activation
130 may be linked to individual variations in working memory (WM) span; the reaching of a
131 resource ceiling could be associated with a subjective WM span. Yet, the few studies
132 assessing the brain activation in reaching and navigational space have only focused on a
133 young population (Toepper et al., 2010; Nemmi et al., 2013), and little is known about age-
134 related compensation and the brain mechanisms supporting VSWM in both spaces.
135

136 This lack of literature is probably due to the technical limitations of neuroimaging systems in
137 real conditions. Recent advances in mobile brain imaging, such as functional Near-Infrared
138 Spectroscopy (fNIRS), allow new opportunities in spatial cognition and navigation studies
139 (Park, Dudchenko & Donaldson, 2018). fNIRS allows to measure local variations of
140 haemoglobin concentration changes related to neuronal activity by the phenomenon of
141 neurovascular coupling (Perrey, 2008). The cortical activity in stimulated area increases the
142 oxygen demand. Oxygen is carried by the haemoglobin. Thus, the local vasculature responds
143 by flooding the cortical area and surrounding tissue with oxygenated form of haemoglobin
144 (ΔO_2Hb) usually accompanied with a concomitant drop in its deoxygenated form (ΔHHb).
145 The fNIRS allows to measure cerebral oxygenation *in situ* with a significant temporal
146 resolution (Perrey, 2008). Besides, this tool seems robust in measuring functional activity
147 during cognitive tasks, as the result of prefrontal cortex activation is similar to magnetic
148 resonance imaging (Cui, Bray, Bryant, Glover, & Reiss, 2011). This device is currently used
149 to examine the neural control of gait in real walking conditions (Perrey, 2014). Also, fNIRS
150 may be used to study the effect of age-related brain activity in VSWM tasks, and more
151 globally in spatial navigation.

152

153 The main objective of this pilot-study was to assess the effect of age on cerebral oxygenation
154 in VSWM tasks according to space (reaching or navigational). A secondary objective of this
155 study was to determine if EF and cerebral oxygenation were involved in VSWM, either in
156 reaching or navigational space. We hypothesized that: i) YA would show a better VSWM
157 performance and therefore higher cerebral oxygenation than OA resulting in a stronger
158 increase of ΔO_2Hb concentration and a stronger decrease in ΔHHb concentration, and ii)
159 performances in cognitive tests would be explicative variables of VSWM performances,
160 especially for navigational space.

161 **2. Material and methods**

162 *2.1 Population*

163 Fifty-five participants were recruited in this cross-sectional study, including 31 YA and 24
164 healthy OA. The inclusion criteria were: i) age between 18 and 35 years old for YA and over
165 65 for OA, ii) fluency in the French language. Exclusion criteria were: i) motor, sleep and
166 perception (visual and auditive) disorders, ii) the presence of depressive symptoms (mini
167 Geriatric Depression Scale (GDS) score >1), cognitive impairment (Mini Mental State
168 Examination (MMSE) score <24), an amnesic complaint, the history or presence of
169 neurological and/or psychiatric diseases, and the use of medications altering memory or
170 cognitive functions. Written informed consent was obtained from each participant, and this
171 study was conducted in accordance with the ethical standards set forth in the Declaration of
172 Helsinki (1983).

173 *2.2 Experimental design*

174 The experimental protocol was divided into two phases: i) VSWM performance assessment
175 in reaching space (i.e., e-CBT: electronic Corsi Block Tapping-test) and in navigational space
176 (i.e., VWCT: Virtual Walking Corsi Task), ii) the administration of a battery of
177 neuropsychological tests. The test administration order was randomized by a computed
178 random number generator algorithm.

179 *2.2.1 VSWM performance assessment*

180 The e-CBT and VWCT conditions were based on Perrochon et al. (2018) (**Figure 1: A and**
181 **B**). A main difference with the original study is that in the present study the participant
182 performed the e-CBT while standing up. In both tests, the participant had to memorize

183 (encoding phase) a sequence of blocks successively lighting up in red. After a computer-
184 generated audible signal marking the end of the sequence, the participant had to reproduce
185 (restitution phase) the sequence in the same order. The number of items gradually increased
186 from 2 to 9. The participant had 2 trials per sequence length. If he succeeded in reproducing
187 one of the two sequences, the sequence length increased by one item (Berch, Krikorian &
188 Huha, 1998). If the participant failed in both trials, the test ended and his span score was the
189 number of items in the last sequence successfully reproduced.

190

191 In reaching space (i.e., the e-CBT), the participant stood in front of the computer screen in
192 order to maintain the same head angle as during the encoding phase of VWCT and thus to
193 ensure the reliability of the fNIRS measurement (**Figure 1: A**). The computer was mounted at
194 700 mm on a table adjusted (min = 90 cm; max = 120 cm) according to the participant's
195 height. The e-CBT sequences were displayed on a 15-inch computer screen. In this situation,
196 the participant had to point out the blocks one after the other by touching the computer screen
197 in order to reproduce the sequence. Although the screen was close to vertical and the floor
198 (VWCT) was horizontal, we ensured, by the angle of the computer screen, that the participant
199 maintained the same visual direction as much as possible (**Figure 1: A and B**).

200

201 For navigational space (i.e., VWCT), we used the "Virtual Carpet"TM developed by A.
202 Berthoz and M. Zaoui, previously described in Perrochon et al. (2018). The participant stood
203 on a starting point 1500 mm away from the test projection space during the encoding phase
204 (**Figure 1: B**). During the restitution phase, the participant had to walk on the numbered
205 blocks in the same order as the presentation, beginning from the starting point and returning
206 to it when finished. The projection space (W316ST Optoma® projector, Taiwan) was 3000

207 mm x 2400 mm (scale 1:10 in regards to the e-CBT) and reproduced the same layout as the e-
208 CBT (**Figure 1: C**).

209 ----- Insert Figure 1 about here -----

210 Participants were wearing an fNIRS device (Portalite®, Artinis Medical, Netherlands) during
211 VSWM tasks. The device consists of two bilateral optodes positioned on the right (Fp2) and
212 left (Fp1) dorsolateral areas of the prefrontal lobe (EEG 10-20 system). Both optodes were
213 connected to an independent portable battery maintained by armbands (**Figure 1**). During the
214 baseline measurements and encoding of the sequences, the participant was asked to limit head
215 movements in order to avoid motion artefacts. In support of this, we ensured that the
216 participant could have a global vision of the entire test layout from the starting point without
217 having to move his head.

218 *2.2.2 Cognitive functions assessment*

219 The participants performed a neuropsychological test battery to measure executive
220 functioning. We used the ZOO map test part A (Wilson, Evans, Emslie, Alderman, &
221 Burgess, 1998) which assesses planning abilities. The participant is asked to navigate through
222 a zoo map while sticking to instructions on places to visit and their order, the variable was the
223 score. We used the Trail Making Test (TMT) (Reitan & Wolfson, 1985) which assesses
224 mental flexibility (part B) and attention (part A) as well as visuo-spatial exploration. The
225 participant must connect in ascending order circles containing numbers from 1 to 25 in part A,
226 whereas he alternate between numbers of letters in part B. For TMT we measured time and
227 the number of errors. We also used REY's figure (Rey, 1941) for planning function, attention
228 and working memory. Participant was asked to copy a figure, without knowing he would be
229 asked to reproduce it after a quick distraction. The score was based on the number of correct
230 reproduced items of the figure for both copy and retrieval conditions. To measure inhibition,

231 we used the Stroop test (Stroop, 1935) consisting in three conditions: naming the colours of
232 squares, reading words of colours in black ink, and naming the ink colour while inhibiting the
233 non-congruent word reading (interference condition). We measured time for the three
234 conditions. In addition to these executive functioning tests, we used the redrawn Mental
235 Rotation Test (MRT) to assess mental rotation capabilities (Peters et al., 1995). In MRT the
236 participant is asked to determine which two of a four sample stimuli are rotated versions of a
237 target stimulus; we measured the score on 24 items. The order of neuropsychological tests
238 was randomized to avoid biases related to cognitive fatigue.

239 *2.3 Outcomes*

240 The main outcome was bilateral dIPFC activation measured by fNIRS and calculated by the
241 change in oxygenated and deoxygenated haemoglobin relative concentration (respectively
242 ΔO_2Hb and ΔHHb) (*Acquisition Software* – Oxysoft® version 3.0.97.1). The Differential
243 Pathlength Factor was calculated from the age of YA and set by default to 5 for OA (Duncan
244 et al., 1996). A baseline was performed before e-CBT and VWCT: the participant had to stare
245 at a red cross located in the centre of the test's layout (i.e., the screen in e-CBT and the carpet
246 in VWCT) for a 20-second period. The baseline was done while standing in front of the
247 screen in e-CBT and on the starting point in VWCT, in order to maintain the same angle of
248 the head in both conditions (**Figure 1: A and B**). We assessed *dIPFC oxygenation only*
249 *during the encoding of the sequences*, as head motion during the restitution phase was
250 producing significant artifacts. Since there were two sequences of encoding for the span score
251 in each test, we computed the mean oxygenation in both sequences. We used Matlab-based
252 scripts when needed for detection and correction of motion artifacts, and a 0.1 Hz low-pass
253 filter was used to remove physiological and instrumental noise (Fishburn, Ludlum, Vaidya, &
254 Medvedev, 2019). We obtained the relative concentration changes in oxyhaemoglobin

255 ($\Delta\text{O}_2\text{Hb}$) and deoxyhaemoglobin (ΔHHb) ($\mu\text{mol.L}^{-1}$) in the selected interval of the test (i.e.,
256 the last 10 seconds), which was normalized by subtracting the mean values of the last 10
257 seconds of baseline from them. According to CRUNCH, we measured those parameters
258 during the encoding of the 4th span and failure span in order to have two points of comparison
259 for patterns of activation (over-recruitment vs. under-recruitment). The 4th span was chosen to
260 assess dlPFC oxygenation at a low/intermediate cognitive load, due to the fNIRS temporal
261 resolution; dlPFC oxygenation measurements in loads lower than the 4th span were not
262 available. Indeed, a systematic methodology-focused study have enlightened a certain delay
263 ($\approx 6\text{s}$) between stimulus presentation and cortical hemodynamic response (Herold et al.,
264 2018). In addition, we need the last 10s during the encoding phase for signal analysis. For this
265 reason, we cannot analyse span 3 or lower (14s duration). The failure span was chosen in
266 order to assess prefrontal oxygenation during the subjective resource ceiling, in accordance
267 with the Schneider-Garces et al. (2010) findings.

268

269 The secondary outcomes were span scores in VSWM and cognitive performance. In e-CBT,
270 the sequence validation was approved by the experimenter, while it was computerized in
271 VWCT. During VWCT, the participant had to wear two motion trackers (HTC® Vive
272 Tracker, HTC, Taiwan) coupled with the base stations (HTC® Vive Lighthouse). The entire
273 device was connected to the RigidBodyViewer Software (Collège de France, Paris, France)
274 (**Figure 1: B**). For neuropsychological tests, we focused on the raw scores in MRT, ZOO,
275 REY, Stroop and TMT.

276 *2.4 Statistical analysis*

277 The normality of our variables data was verified with a Shapiro-Wilk test. Student tests were
278 used in order to compare the socio-demographic variables and neuropsychological scores

279 between both groups. We performed a 2*2 mixed ANOVA with the two populations (OA vs.
280 YA) and the two spaces (VWCT vs. e-CBT) to study their effect on the VSWM span score.
281 We also conducted 2*2 mixed ANOVAs with the two age groups (YA vs. OA) and the two
282 spaces (VWCT vs. e-CBT) in order to study their effect on cerebral oxygenation parameters
283 during the encoding of the 4th span and failure span. Univariable linear regressions were
284 performed to examine relationships between cerebral oxygenation parameters and cognitive
285 function capabilities (independent variables) and span scores in e-CBT and VWCT
286 (dependent variable). Separate multivariable linear regressions by stepwise method were run
287 to examine whether cognitive function variables and cerebral oxygenation parameters would
288 explain VSWM performance in different spaces. For all analyses, the statistical significance
289 level was set at alpha <0.05. The statistical analysis was performed using IBM SPSS®
290 Statistics version 22 (IBM Corp, Armonk, USA).

291 **3. Results**

292 55 participants were included in this study: 31 YA (22.8 ± 2.8 years; 19 female) and 24 OA
293 (70.4 ± 3.7 years; 17 female). Socio-demographic and cognitive capabilities are presented in
294 **Table 1**. We observed a decreased cognitive performance in OA (vs. YA) in many
295 neuropsychological tests, such as the MRT, ZOO, REY, TMT and STROOP ($p < 0.05$).

296

297 We also observed through the age*space ANOVA on span scores an overall effect of age,
298 with YA showing higher span scores than OA (respectively 7.0 ± 0.2 vs. 5.1 ± 0.2 ; $F(1,53) =$
299 39.657 ; $p < 0.001$). We also found an overall effect of space, as participants showed better span
300 scores in reaching space compared to navigational space (respectively 6.5 ± 0.2 vs. 5.5 ± 0.2 ;
301 $F(1,53) = 55.496$; $p < 0.001$) (**Figure 2**). We found no significant age*space interaction effect
302 on VSWM span scores ($p > 0.05$).

303

304 -----Insert Figure 2 and Table 1 about here -----

305 *3.1 Effects of ageing on cerebral oxygenation in VSWM tasks*

306 -----Insert figure 3 about here-----

307 ANOVA on dlPFC oxygenation during the 4th span encoding revealed no main effects of age
308 and space and no interaction effects for the ΔO_2Hb value ($p > 0.05$; **Figure 3: A**), but an
309 age*space interaction effect for ΔHHb ($F(1,53) = 4.35$; $p < 0.05$; **Figure 3: B**). Post hoc
310 analysis revealed a significantly lower ΔHHb value for YA compared to OA only in
311 navigational space (respectively -0.7 ± 1.2 vs. $-0.1 \pm 1.2 \mu\text{mol.L}^{-1}$, $p < 0.05$). We also observed
312 a significantly higher ΔHHb concentration in navigational space compared to reaching space
313 among OA (respectively -0.1 ± 1.2 vs. $-0.7 \pm 1.2 \mu\text{mol.L}^{-1}$, $p < 0.05$, **Figure 3: B**).

314

315 For the failure span encoding, we observed an overall effect of age, with YA showing higher
316 $\Delta\text{O}_2\text{Hb}$ concentration than OA (respectively 6.3 ± 0.5 vs. $3.8 \pm 0.6 \mu\text{mol.L}^{-1}$, $F(1,53) = 11.07$;
317 $p < 0.01$). We also found an overall effect of space, with participants showing higher $\Delta\text{O}_2\text{Hb}$
318 values in reaching space compared to navigational space (respectively 6.2 ± 0.6 vs. 3.8 ± 0.5
319 $\mu\text{mol.L}^{-1}$, $F(1,53) = 7.36$; $p < 0.01$; **Figure 3: C**). However, we did not find any significant
320 age*space interaction effect ($p > 0.05$). Finally, we found a significant age*space interaction
321 effect on the ΔHHb concentration ($F(1,53) = 6.90$; $p < 0.05$). Post hoc analysis revealed a
322 significant difference between groups only in navigational space, with a lower ΔHHb
323 concentration for YA compared to OA (respectively -1.7 ± 2 vs. $-0.3 \pm 1.4 \mu\text{mol.L}^{-1}$, $p < 0.05$).
324 Post hoc also revealed that only OA showed significant differences of ΔHHb between both
325 spaces, with a lower value in reaching space compared to navigational space (respectively -
326 0.3 ± 1.4 vs. $-1.3 \pm 1.3 \mu\text{mol.L}^{-1}$, $p < 0.05$, **Figure 3: D**).

327

328 *3.2 Association between dlPFC activation and VSWM performance*

329

330 -----Insert table 2 about here-----

331 For the e-CBT, the span score showed a positive correlation only with the dlPFC $\Delta\text{O}_2\text{Hb}$
332 during failure span encoding ($r = 0.32$, $p < 0.05$, **Table 2**). For the VWCT, the span score was
333 associated with more oxygenation parameters such as ΔHHb concentration during the 4th span
334 encoding and failure span encoding ($r = -0.34$; $p < 0.05$, $r = -0.50$; $p < 0.001$ respectively) and
335 with the dlPFC $\Delta\text{O}_2\text{Hb}$ during the failure span encoding ($r = 0.31$; $p < 0.05$).

336 *3.3 Cognitive functions involved in VSWM according to space*

337 Most of the neuropsychological tests, such as MRT ($r = 0.64$; $p < 0.001$), ZOO ($r = 0.45$;
338 $p < 0.001$), REY R ($r = 0.60$; $p < 0.001$), STROOP I ($r = -0.63$; $p < 0.001$), TMT A ($r = -0.54$;

339 $p < 0.001$), TMT B ($r = -0.40$; $p < 0.01$) and Δ TMTs ($r = -0.28$; $p < 0.05$) were associated with the
340 span score in reaching space (**Table 2**). Similarly, MRT ($r = 0.68$; $p < 0.001$), ZOO ($r = 0.34$;
341 $p < 0.05$), REY R ($r = 0.59$; $p < 0.001$), STROOP I ($r = -0.54$; $p < 0.001$), TMT A ($r = -0.49$;
342 $p < 0.001$) and TMT B ($r = -0.33$; $p < 0.05$) were associated with the span score in navigational
343 space.

344 3.4 Stepwise regression model

345 By performing stepwise regression, including age, level of education, sex, MRT, ZOO, REY
346 R, STROOP I and TMT B and dlPFC oxygenation parameters, we found associations between
347 the span score and age, MRT ($p < 0.01$) and ZOO ($p < 0.05$) performance in reaching space
348 (**Table 3**). Furthermore, we observed additional associations between the span score and
349 dlPFC oxygenation during failure span encoding (Δ HHb: $p < 0.05$), MRT ($p < 0.001$) and REY
350 ($p < 0.05$) scores in navigational space (**Table 3**). The total variance accounted for these
351 models was strong, while these variables explain 67% of VSWM performance in reaching
352 space and 63% of VSWM performance in navigational space (**Table 3**).

353

354 ----- Insert Table 3 about here -----

355 **4. Discussion**

356 This is the first study assessing the age-related effect on cerebral oxygenation and the
357 association of cognitive capabilities with VSWM according to space. We observed a
358 significant difference of cerebral oxygenation depending on age, with higher dIPFC activation
359 (i.e., decreased ΔHHb) for YA compared to OA when the participant was encoding the
360 subsequent task in navigational space. dIPFC activation seems to be associated with VSWM
361 performance, specifically in the navigational task. Finally, different EF (i.e., mental rotation,
362 planning capabilities, attention) are associated with VSWM performance according to space.

363 *4.1 Effect of ageing on cerebral oxygenation in VSWM*

364 First, we observed an effect of ageing on VSWM performance, as YA outperformed OA.
365 These results match findings of other studies, which demonstrated age-related deficits in
366 VSWM performances in similar paradigms (Piccardi et al., 2011, 2013; Perrochon et al.,
367 2014, 2018).

368

369 In navigational space, we found that YA showed a stronger dIPFC activation (i.e., decrease of
370 ΔHHb) compared to OA during the encoding phase in navigation space (4th span and failure
371 span in VWCT). The decrease of ΔHHb is a typical intravascular oxygenation response to
372 brain activity (Villringer, Planck, Hock, Schleinkofer & Dirnagl, 1993; Scholkmann et al.,
373 2014; Buxton, 2012). Thus, in our framework, OA showed an under-activation of dIPFC
374 compared to YA. Whereas it seems coherent for the failure span, this under activation pattern
375 is already appearing at 4th span. It may be related to behavioural data, since OA reached on
376 average their VWCT span score at 4.6 ± 0.8 and the mode span score of the OA distribution
377 was 4 (14 participants out of 24). As the reaching of a resource ceiling has been found to be
378 individually WM load dependant (Schneider-Garces et al., 2010 ; Cappell, Gmeindl & Reuter-

379 Lorenz, 2010), we can suppose that most of the OA have reached this resource ceiling around
380 4th span, and are no longer able to compensate, leading to under activation pattern. These
381 results corroborate partly with the CRUNCH model (Reuter-Lorenz & Cappell, 2008), since
382 we observed an under-activation of OA compared to YA at high levels of cognitive load.

383 At higher levels of cognitive load, OA processing capacity limits are reached, and processing
384 areas show less activity than those of YA, as compensatory mechanisms of the functional
385 deficiency may no longer be effective. The decrease in ΔHHb during encoding was
386 associated to VSWM behavioural performance in VWCT. These data add evidence to the
387 observed age-related effects (weaker ΔHHb decrease) and allow us to assume that OA dlPFC
388 under-activation during the encoding of the sequences may be directly involved in their
389 poorer performance.

390 The lower spans (2 and 3) were not usable given their short duration and the delay between
391 stimulus presentation and hemodynamic response. However, low levels of cognitive load
392 remain to be investigated for proof of age-related overactivation by adapting the task to
393 fNIRS data processing.

394

395 Overall, ΔHHb was more affected by age-related effects and associated with VSWM
396 performance in navigational space, whereas $\Delta\text{O}_2\text{Hb}$ was not. ΔHHb is more affected by
397 oxygen consumption than $\Delta\text{O}_2\text{Hb}$, and therefore is a better indicator of activation than $\Delta\text{O}_2\text{Hb}$
398 (Scholkmann et al., 2014). However, $\Delta\text{O}_2\text{Hb}$ is often described as a more reliable indicator for
399 functional brain activity because of its higher amplitude, and is less sensitive to noise
400 (Strangman Culver, Thompson & Boas, 2002; Wolf et al., 2011). Still, ΔHHb is a reliable
401 indicator of functional activation, and we followed the Fishburn et al. (2019) correction
402 method to remove noise effects from the signal. There may possibly be non-neuronal driven
403 changes in haemodynamic, such as physiological confounders in the signal which might

404 influence our results. This is an issue for all haemodynamic-based functional brain imaging
405 techniques. Nevertheless, most of the recommended guidelines, from the design of the
406 protocol to fNIRS instrumentation and analysis approaches to avoid false positives/negatives,
407 were followed (Tachtsidis & Scholkmann, 2016).

408

409 The age-related under-activation during encoding could be linked to poorer cognitive
410 strategies use by OA to encode the stimuli in memory and to plan restitution, hence leading to
411 the recruitment of inaccurate cerebral areas (Reuter-Lorenz & Lustig, 2005; Logan et al.,
412 2002). OA often fail to use controlled and costly processing strategies to support their
413 performance. EF are required in acquiring new skills, selecting appropriate strategies,
414 planning the execution of the task, monitoring behavioural responses and finding alternative
415 strategies if the selected one is not efficient (West, 1996). We observed deficits in most of the
416 assessed EF and their association to performance in VWCT. Considering these
417 observations, we could hypothesize that under-activation during encoding in navigational
418 space could result from the use of inefficient cognitive strategies mediated by the age-related
419 decline in EF. Further studies are needed to investigate this hypothesis as we did not
420 demonstrate it clearly. Except its role in executive functioning and VSWM, the dlPFC may
421 also be implied in processing the movement along a learned route in a navigational
422 environment, as it would be involved in the processing of self-generated locomotor
423 movements and of strategy related to motor imagery (Berthoz, 1997; Nemmi et al., 2013).
424 This study thus highlights the major role of prefrontal circuits in age-related performance in
425 VSWM. .

426

427 Age differences in cerebral activation were only observed in navigational space. Since dlPFC
428 has been specifically linked with navigational space and not reaching space (Nemmi et al.,

429 2013), we can assume that it may explain why dlPFC oxygenation differences between our
430 populations is only discriminated in VWCT. However, we found an overall effect of space on
431 ΔO_2Hb , with higher concentration values in reaching space compared to navigational space
432 during failure span encoding. Thus, dlPFC oxygenation seems to be stronger in reaching
433 space. It may be load-dependent, since reaching space allows better performances for both our
434 populations than navigational space, which is known to be more complex and requires more
435 resources (Röser, Hardiess, & Mallot, 2016). Nevertheless, we did not find ΔO_2Hb to be
436 linked with VSWM performance. Another result contrasts with the observations of Nemmi et
437 al. (2013), as we found that ΔHHb was different in OA, with a stronger decrease in reaching
438 space compared to navigational space. However, the observations of Nemmi et al. (2013)
439 were only done in a study of a young adult population (mean age 24.7 ± 4.5), and we cannot
440 state that tests in both spaces lie on a distinct neural basis exactly in the same way as in the
441 OA population. Thus, dlPFC may play a role in better performances of OA in reaching space
442 compared to navigational space; however, we did not find ΔHHb to be linked with
443 performance in reaching space and it remains to be investigated.

444 *4.2 Cognitive correlates of space*

445 We had assumed that raw scores on cognitive tests would be more associated to VSWM
446 performance in navigational space because of the more active and complex nature of this task
447 compared to the VSWM task in reaching space (Piccardi et al., 2008, 2013, 2014; Nori et al.,
448 2015). Our results would not allow us to confirm this hypothesis, as we observed that both
449 spaces imply distinct cognitive processes (see R^2 values in **Table 3**) as well as common
450 processes. Nonetheless, these results highlight the major association of mental rotation with
451 VSWM performances (Gallou-Guyot et al., 2020). Mental rotation may support the updating
452 and mental manipulation of spatial information as the participant is orientating and moving

453 through the environment (Piccardi et al., 2008; Röser et al., 2016). On one hand, the ZOO test
454 (Wilson et al., 1998) evidenced that planning ability was one of the EF associated with
455 VSWM performance in reaching space. On the other hand, the analyses of the Rey figure
456 (Rey, 1941) confirmed the strong association between executive functioning, in the
457 maintenance of spatial information, the selection of appropriate strategies, the control of
458 performance and mental flexibility and VSWM performance in navigational space .

459 Our results allowed us to demonstrate a clear link between executive functioning and VSWM
460 performances in different space. As we observed age-related deficits in all of these cognitive
461 tests (**Table 1**) and a relation between dlPFC oxygenation and VSWM performance, we
462 could suppose that the decline of EF could partly explain the poorer VSWM performance in
463 ageing through their potential role in strategy production in navigational space . In such case
464 it would support the executive hypothesis of cognitive ageing, that age-related memory
465 differences and global decline in cognition may be mediated by the prefrontal area
466 deterioration that supports WM and EF (West, 1996; Raz, 2000). However, we have no proof
467 that EF effectively mediate the age-related variance in VSWM performance. The nature of the
468 relation between age and VSWM performances and how executive functioning mediate this
469 relation thus need to be developed to provide empirical evidences for the executive hypothesis
470 of cognitive ageing.

471 To summarise, VSWM performances in navigational space were associated with prefrontal
472 Δ HHb concentration during the encoding of sequences, and appear to be associated with
473 ageing, mental rotation abilities and Rey's figure performances, whereas reaching space
474 VSWM performances were associated with mental rotation abilities and ZOO test
475 performances.

476 *4.3 Limitations*

477 Several limitations should be considered in future studies. First, fNIRS acquisition could only
478 be done during the encoding phase of the sequences, due to the great number of head rotations
479 and movements during the restitution phase in navigational space that induced large motion
480 artefacts in the signal. Nevertheless, it has been demonstrated by means of EEG power
481 analysis that encoding of visuo-spatial information is more cognitively challenging than
482 retrieval because it requires more cerebral efforts (Jaiswal, Ray & Slobounov, 2010).
483 Moreover, as being said fNIRS analysis could not be done for low spans and thus they still
484 need to be studied to demonstrate if patterns of cerebral activation really fit with CRUNCH
485 model. Second, despite its important temporal resolution, fNIRS cannot be used to investigate
486 deep brain structures involved in spatial memory, such as the hippocampus (Maguire et al.,
487 1998; Lithfous et al., 2013; Latini-Corazzini et al., 2010) . We were also limited to two
488 optodes in this study thus, we could not assess the lateralization effect. Since our device was
489 not a multi-channel fNIRS, we were not able to investigate the involvement of the parietal
490 cortex, which is a key structure in spatial working memory (Constantinidis & Wang, 2004).
491 Furthermore, because of the switch of engaged brain areas due to ageing from posterior to
492 more anterior structures (PASA model) (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2007), it
493 would be relevant in future studies to investigate the effects of age on parietal cortex
494 activation. Third, cognitive tests allowed us to identify several implied cognitive functions
495 such as mental rotation and EF in VSWM tasks, but this work remains to be conducted with
496 more varied cognitive tests, as we limited them to avoid cognitive fatigue.

497 *4.4 Perspectives*

498 This research takes part in the investigation of brain mechanisms that tend to decline in ageing
499 and may be essential factors in age-related deficits in VSWM . VWCT could be used in the
500 early detection of spatial memory impairment, such as in the dementias (Iachini et al., 2009).

501 This study could be reproduced in those with neurological pathologies such as stroke, in
502 which brain damage leads to different haemodynamic responses (Hermand et al., 2019).
503 Finally, fNIRS could be used in complex navigation tests (Perrochon et al., 2014) to reflect
504 the involvement of EF in these tasks.

505 *5. Conclusion*

506 This study demonstrated that healthy OA seem to have less activation of their dlPFC
507 compared to YA in VSWM tasks. This dlPFC activation seems to be associated with VSWM
508 performance, particularly in navigational space . Finally, we identified the major association
509 of some cognitive functions, such as mental rotation and EF with VSWM performance in
510 reaching and navigational spaces.

511 **Author contributions**

512 TK: Conceptualization and methodology, data acquisition and analysis, manuscript drafting;
513 EH: Methodology, formal analysis, and manuscript review; AB: Conceptualization, software
514 and manuscript review; AC and MGG : Methodology and manuscript review; JCD:
515 Resources, conceptualization, manuscript review; AP: Conceptualization and methodology,
516 data analysis, supervision, resources, manuscript drafting.

517 **Declarations of interest**

518 None

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522 **References**

523

524 Baddeley, A. (1998). Recent developments in working memory. *Current opinion in*

525 *neurobiology*, 8(2), 234-238.

526 Belmonti, V., Berthoz, A., Cioni, G., Fiori, S., & Guzzetta, A. (2015). Navigation strategies as

527 revealed by error patterns on the Magic Carpet test in children with cerebral palsy. *Frontiers*

528 *in psychology*, 6, 880.

529 Berch, D. B., Krikorian, R., & Huha, E. M. (1998). The Corsi block-tapping task:

530 Methodological and theoretical considerations. *Brain and cognition*, 38(3), 317-338.

531 Berthoz, A. (1997). Parietal and hippocampal contribution to topokinetic and topographic

532 memory. *Philosophical Transactions of the Royal Society of London. Series B: Biological*

533 *Sciences*, 352(1360), 1437-1448.

534 Berthoz, A., & Viaud-Delmon, I. (1999). Multisensory integration in spatial

535 orientation. *Current opinion in neurobiology*, 9(6), 708-712.

536 Buxton, R. B. (2012). Dynamic models of BOLD contrast. *Neuroimage*, 62(2), 953-961.

537 Cappell, K. A., Gmeindl, L., & Reuter-Lorenz, P. A. (2010). Age differences in prefrontal

538 recruitment during verbal working memory maintenance depend on memory

539 load. *Cortex*, 46(4), 462-473.

540 Constantinidis, C., & Wang, X. J. (2004). A neural circuit basis for spatial working

541 memory. *The Neuroscientist*, 10(6), 553-565.

542 Corsi, P. M. (1972). Human memory and the medial temporal region of the brain.

543 *Dissertation Abstracts International*, 34, 819B.

544 Craik, F. I., & Salthouse, T. A. (Eds.). (2011). *The handbook of aging and cognition*.

545 Psychology press.

546 Cui, X., Bray, S., Bryant, D. M., Glover, G. H., & Reiss, A. L. (2011). A quantitative
547 comparison of NIRS and fMRI across multiple cognitive tasks. *Neuroimage*, *54*(4), 2808-
548 2821.

549 Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during
550 working memory. *Trends in cognitive sciences*, *7*(9), 415-423.

551 Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2007). Que PASA?
552 The posterior–anterior shift in aging. *Cerebral cortex*, *18*(5), 1201-1209.

553 Duncan, A., Meek, J. H., Clemence, M., Elwell, C. E., Fallon, P., Tyszczuk, L., ... & Delpy,
554 D. T. (1996). Measurement of cranial optical path length as a function of age using phase
555 resolved near infrared spectroscopy. *Pediatric research*, *39*(5), 889.

556 Fishburn, F. A., Ludlum, R. S., Vaidya, C. J., & Medvedev, A. V. (2019). Temporal
557 Derivative Distribution Repair (TDDR): A motion correction method for
558 fNIRS. *NeuroImage*, *184*, 171-179.

559 Hermand, E., Tapie, B., Dupuy, O., Fraser, S. A., Compagnat, M., Salle, J. Y., ... &
560 Perrochon, A. (2019). Prefrontal cortex activation during dual task with increasing cognitive
561 load in subacute stroke patients: A pilot study. *Frontiers in Aging Neuroscience*, *11*, 160.

562 Herold, F., Wiegel, P., Scholkmann, F., & Müller, N. G. (2018). Applications of functional
563 near-infrared spectroscopy (fNIRS) neuroimaging in exercise–cognition science: a systematic,
564 methodology-focused review. *Journal of clinical medicine*, *7*(12), 466.

565 Iachini, T., Iavarone, A., Senese, V. P., Ruotolo, F., & Ruggiero, G. (2009). Visuospatial
566 memory in healthy elderly, AD and MCI: a review. *Current aging science*, *2*(1), 43-59.

567 Jaiswal, N., Ray, W., & Slobounov, S. (2010). Encoding of visual–spatial information in
568 working memory requires more cerebral efforts than retrieval: Evidence from an EEG and
569 virtual reality study. *Brain Research*, *1347*, 80-89.

570 Korthauer, L. E., Nowak, N. T., Frahm, M., & Driscoll, I. (2017). Cognitive correlates of
571 spatial navigation: associations between executive functioning and the virtual Morris Water
572 Task. *Behavioural brain research*, 317, 470-478.

573 Latini-Corazzini, L., Nesa, M. P., Ceccaldi, M., Guedj, E., Thinus-Blanc, C., Cauda, F., ... &
574 Péruch, P. (2010). Route and survey processing of topographical memory during
575 navigation. *Psychological research*, 74(6), 545-559.

576 Lithfous, S., Dufour, A., & Després, O. (2013). Spatial navigation in normal aging and the
577 prodromal stage of Alzheimer's disease: insights from imaging and behavioral studies. *Ageing
578 research reviews*, 12(1), 201-213.

579 Logan, J. M., Sanders, A. L., Snyder, A. Z., Morris, J. C., & Buckner, R. L. (2002). Under-
580 recruitment and nonselective recruitment: dissociable neural mechanisms associated with
581 aging. *Neuron*, 33(5), 827-840.

582 Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S., Frith, C. D., & O'Keefe, J.
583 (1998). Knowing where and getting there: a human navigation network. *Science*, 280(5365),
584 921-924.

585 Meneghetti, C., Borella, E., Carbone, E., Martinelli, M., & De Beni, R. (2016). Environment
586 learning using descriptions or navigation: The involvement of working memory in young and
587 older adults. *British Journal of Psychology*, 107(2), 259-280.

588 Nori, R., Piccardi, L., Migliori, M., Guidazzoli, A., Frasca, F., De Luca, D., & Giusberti, F.
589 (2015). The virtual reality walking corsi test. *Computers in Human Behavior*, 48, 72-77.

590 Nemmi, F., Boccia, M., Piccardi, L., Galati, G., & Guariglia, C. (2013). Segregation of neural
591 circuits involved in spatial learning in reaching and navigational
592 space. *Neuropsychologia*, 51(8), 1561-1570.

593 Park, D. C. (2000). The basic mechanisms accounting for age-related decline in cognitive
594 function. *Cognitive aging: A primer*, 11(1), 3-19.

595 Park, J. L., Dudchenko, P. A., & Donaldson, D. I. (2018). Navigation in real-world
596 environments: new opportunities afforded by advances in mobile brain imaging. *Frontiers in*
597 *human neuroscience*, *12*.

598 Perrey, S. (2008). Non-invasive NIR spectroscopy of human brain function during
599 exercise. *Methods*, *45*(4), 289-299.

600 Perrey, S. (2014). Possibilities for examining the neural control of gait in humans with
601 fNIRS. *Frontiers in Physiology*, *5*, 204.

602 Perrochon, A., Kemoun, G., Dugué, B., & Berthoz, A. (2014). Cognitive impairment
603 assessment through visuospatial memory can be performed with a modified walking Corsi test
604 using the 'magic carpet'. *Dementia and geriatric cognitive disorders extra*, *4*(1), 1-13.

605 Perrochon, A., Mandigout, S., Petruzzellis, S., Garcia, N. S., Zaoui, M., Berthoz, A., &
606 Daviet, J. C. (2018). The influence of age in women in visuo-spatial memory in reaching and
607 navigation tasks with and without landmarks. *Neuroscience letters*, *684*, 13-17.

608 Peters, M., Laeng, B., Latham, K., Jackson, M., Zaiyouna, R., & Richardson, C. (1995). A
609 redrawn Vandenberg and Kuse mental rotations test-different versions and factors that affect
610 performance. *Brain and cognition*, *28*(1), 39-58.

611 Piccardi, L., Bianchini, F., Argento, O., De Nigris, A., Maialetti, A., Palermo, L., & Guariglia,
612 C. (2013). The Walking Corsi Test (WalCT): standardization of the topographical memory
613 test in an Italian population. *Neurological Sciences*, *34*(6), 971-978.

614 Piccardi, L., Bianchini, F., Nori, R., Marano, A., Iachini, F., Lasala, L., & Guariglia, C.
615 (2014). Spatial location and pathway memory compared in the reaching vs. walking domains.
616 *Neuroscience Letters*, *566*, 226-230.

617 Piccardi, L., Iaria, G., Bianchini, F., Zompanti, L., & Guariglia, C. (2011). Dissociated
618 deficits of visuo-spatial memory in near space and navigational space: evidence from brain-

619 damaged patients and healthy older participants. *Aging, Neuropsychology, and*
620 *Cognition*, 18(3), 362-384.

621 Piccardi, L., Iaria, G., Ricci, M., Bianchini, F., Zompanti, L., & Guariglia, C. (2008). Walking
622 in the Corsi test: which type of memory do you need?. *Neuroscience Letters*, 432(2), 127-131.

623 Raz, N. (2000). Aging of the brain and its impact on cognitive performance: Integration of
624 structural and functional findings.

625 Reitan, R. M., & Wolfson, D. (1985). *The Halstead-Reitan neuropsychological test battery:*
626 *Theory and clinical interpretation* (Vol. 4). Reitan Neuropsychology.

627 Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive aging and the compensation
628 hypothesis. *Current directions in psychological science*, 17(3), 177-182.

629 Reuter-Lorenz, P. A., & Lustig, C. (2005). Brain aging: reorganizing discoveries about the
630 aging mind. *Current opinion in neurobiology*, 15(2), 245-251.

631 Rey, A. (1941). L'examen psychologique dans les cas d'encéphalopathie traumatique.(Les
632 problems.). *Archives de psychologie*.

633 Röser, A., Hardiess, G., & Mallot, H. A. (2016). Modality dependence and intermodal transfer
634 in the Corsi Spatial Sequence Task: Screen vs. Floor. *Experimental brain research*, 234(7),
635 1849-1862.

636 Schneider-Garces, N. J., Gordon, B. A., Brumback-Peltz, C. R., Shin, E., Lee, Y., Sutton, B.
637 P., ... & Fabiani, M. (2010). Span, CRUNCH, and beyond: working memory capacity and the
638 aging brain. *Journal of cognitive neuroscience*, 22(4), 655-669.

639 Scholkmann, F., Kleiser, S., Metz, A. J., Zimmermann, R., Pavia, J. M., Wolf, U., & Wolf, M.
640 (2014). A review on continuous wave functional near-infrared spectroscopy and imaging
641 instrumentation and methodology. *Neuroimage*, 85, 6-27.

642 Strangman, G., Culver, J. P., Thompson, J. H., & Boas, D. A. (2002). A quantitative
643 comparison of simultaneous BOLD fMRI and NIRS recordings during functional brain
644 activation. *Neuroimage*, 17(2), 719-731.

645 Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of experimental*
646 *psychology*, 18(6), 643.

647 Tachtsidis, I., & Scholkmann, F. (2016). False positives and false negatives in functional
648 near-infrared spectroscopy: issues, challenges, and the way forward. *Neurophotonics*, 3(3),
649 031405.

650 Taillade, M., Sauzéon, H., Dejos, M., Arvind Pala, P., Larrue, F., Wallet, G., ... & N'Kaoua,
651 B. (2013). Executive and memory correlates of age-related differences in wayfinding
652 performances using a virtual reality application. *Aging, Neuropsychology, and*
653 *Cognition*, 20(3), 298-319.

654 Toepper, M., Markowitsch, H. J., Gebhardt, H., Beblo, T., Thomas, C., Gallhofer, B., ... &
655 Sammer, G. (2010). Hippocampal involvement in working memory encoding of changing
656 locations: an fMRI study. *Brain Research*, 1354, 91-99.

657 Villringer, A., Planck, J., Hock, C., Schleinkofer, L., & Dirnagl, U. (1993). Near infrared
658 spectroscopy (NIRS): a new tool to study hemodynamic changes during activation of brain
659 function in human adults. *Neuroscience letters*, 154(1-2), 101-104.

660 West, R. L. (1996). An application of prefrontal cortex function theory to cognitive
661 aging. *Psychological bulletin*, 120(2), 272.

662 Wilson, B. A., Evans, J. J., Emslie, H., Alderman, N., & Burgess, P. (1998). The development
663 of an ecologically valid test for assessing patients with a dysexecutive
664 syndrome. *Neuropsychological rehabilitation*, 8(3), 213-228.

665 Wolbers, T., & Hegarty, M. (2010). What determines our navigational abilities?. *Trends in*
666 *cognitive sciences*, 14(3), 138-146.

667 Wolf, U., Toronov, V., Choi, J. H., Gupta, R., Michalos, A., Gratton, E., & Wolf, M. (2011).
668 Correlation of functional and resting state connectivity of cerebral oxy-, deoxy-, and total
669 hemoglobin concentration changes measured by near-infrared spectrophotometry. *Journal of*
670 *biomedical optics*, 16(8), 087013.

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677 **Figure and Tables**

678 **Figure 1.** Plan of the experimental conditions. The participant is wearing the fNIRS device.
679 The experimental design was intended to maintain the same head angle during both
680 conditions. **A)** e-CBT performed on a computer screen. **B)** VWCT performed on the projected
681 virtual carpet. The participant is wearing two movement tracking sensors on the head and the
682 chest connected to the two HTC base stations attached to the walls. **C)** Test layout.

683

684 **Figure 2.** Span scores means and standard deviations (represented by error bars) in VWCT
685 and e-CBT for older adults (OA) and young adults (YA). Main effects of age (**: $p < 0.001$)
686 and space (++++ **: $p < 0.001$) were represented.

687

688 **Figure 3.** dlPFC oxygenation means and standard deviations (represented by error bars) for
689 older adults (OA) and young adults (YA) in reaching and navigational space for 4th span and
690 failure span. **A)** ΔO_2Hb during the encoding of 4th span. **B)** ΔHHb during the encoding of 4th
691 span. We represented differences between YA and OA in VWCT (*: $p < 0.05$) and space effect
692 for the OA group (* *: $p < 0.05$). **C)** ΔO_2Hb during the encoding of failure span. Main effects of
693 age (++ **: $p < 0.01$) and space (### **: $p < 0.01$) are represented. **D)** ΔHHb during the encoding of
694 failure span. We represented significant differences between YA and OA in VWCT (*:
695 $p < 0.05$) and space effect for OA group (* *: $p < 0.05$).

696

697 **Table 1.** Demographic, psychologic, and cognitive characteristics of the study participants.

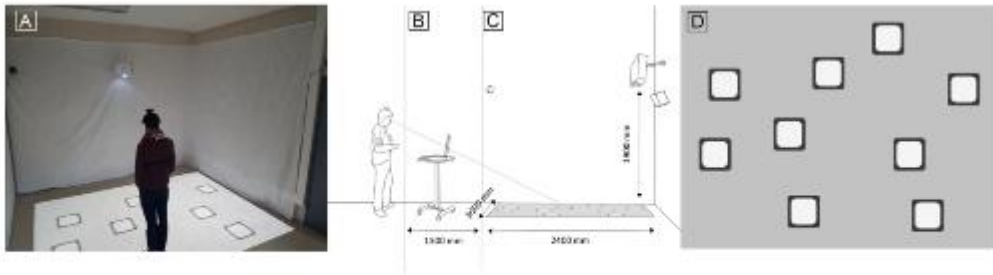
698

699 **Table 2.** Correlations between raw scores in cognitive tests and VSWM tasks and
700 oxygenation parameters in 4th span and failure span.

701

702 **Table 3.** Regression analysis for the variables identified as correlated to VSWM tasks.

703



704 **Fig. 1.** Plan of the experimental conditions. The participant is wearing the fNIRS device. The experimental design was intended to maintain the same head angle during both conditions. A) Picture of the experimental environment, VWCT is being performed by a participant. B) e-CBT performed on a computer screen. C) VWCT performed on the projected virtual carpet. The participant is wearing two movement tracking sensors on the head and the chest connected to the two HTC base stations attached to the walls. D) Test layout.

Table 1

Demographic, psychologic, and cognitive characteristics of the study participants.

	Variables (unity) or [rank]	Young adults (n = 31)	Older adults (n = 24)	P value
Demographic, psychologic and cognitive characteristics	Age (years)	22.8 ± 2.8 [19;31]	70.4 ± 3.7 [65;80]	<0.001
	Female (%)	61.3 % (n = 19)	70.8 % (n = 17)	0.47
	Educational level	3.0 ± 0	3.3 ± 1.4	0.19
	MMSE [0–30]		28.2 ± 1.5	
	GDS [0–4]	0.1 ± 0.2	0.1 ± 0.3	0.79
	Female hormonal cycle	5.3 % (n = 1)		
Cognitive tests:				
Mental Rotation	MRT [0–24]	5.9 ± 3.7	2.2 ± 1.5	<0.001
Planning	ZOO [max 8]	6.1 ± 2.8	3.9 ± 3.2	<0.001
Attention. WM. Planning	REY C [0–36]	35.7 ± 0.6	35.2 ± 1.4	0.07
	REY R [0–36]	25.9 ± 4.9	18.0 ± 6.2	<0.001
Inhibition	STROOP D (s)	50.6 ± 7.1	66.6 ± 12.9	<0.001
	STROOP R (s)	37.9 ± 5.2	47 ± 8.7	<0.001
	STROOP I (s)	79.6 ± 17	132.1 ± 30.2	<0.001
	ΔSTROOP (I–D) (s)	28.9 ± 16.4	65.4 ± 21	<0.001
Cognitive flexibility. Visuo-spatial exploring	TMT A (s)	22.1 ± 6.9	40.1 ± 14.6	<0.001
	TMT B (s)	50.5 ± 18.4	87.6 ± 59.2	<0.01
	Δ TMTs (B–A)	28.4 ± 18.2	47.5 ± 51.4	0.06
	Errors TMT A (n.u)	0.1 ± 0.2	0.1 ± 0.3	0.45
	Errors TMT B (n.u)	1.5 ± 3.7	2.1 ± 3.4	0.49

Mean ± SD and range [minimum;maximum].

MMSE = Mini Mental State examination; GDS = Geriatric Depression Scale; MRT = Mental Rotation Test; REY C = Rey copy; REY R = Rey restitution; STROOP D = Denomination; STROOP R = Reading; STROOP I = Interference; TMT = Trail Making Test; WM = Working Memory. Data written in bold show an effect of aging on variables.

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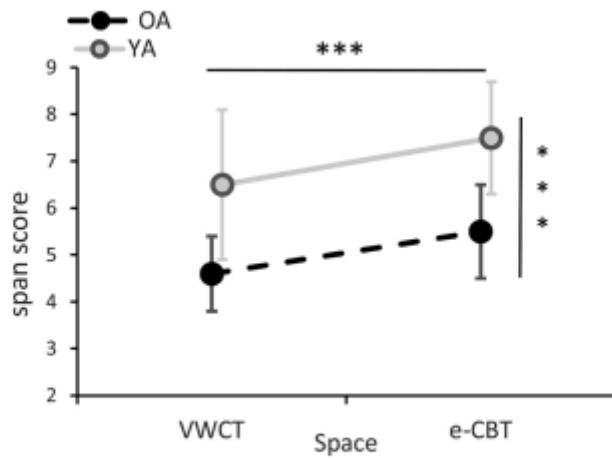


Fig. 2. Span scores means and standard deviations (represented by error bars) in VWCT and e-CBT for older adults (OA) and young adults (YA). Main effects of age (***) : $p < 0.001$ and space (***) : $p < 0.001$ were represented.

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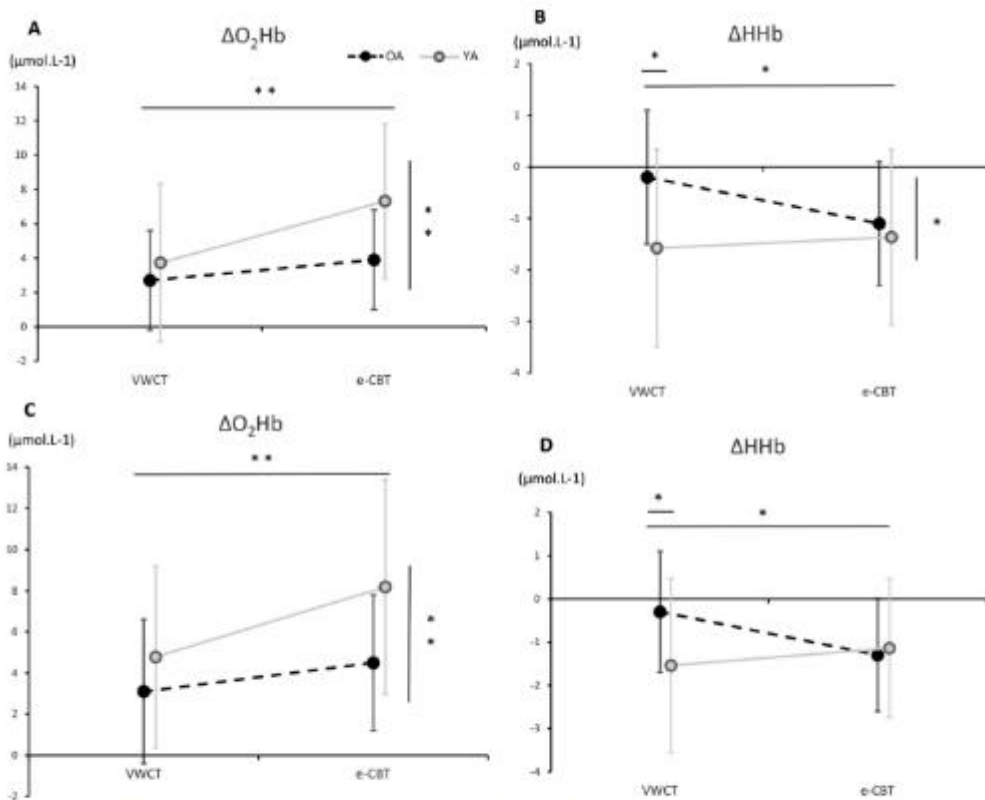


Fig. 3. DIPFC oxygenation means and standard deviations (represented by error bars) for older adults (OA) and young adults (YA) in reaching and navigational space for maximum span and failure span. **A)** $\Delta\text{O}_2\text{Hb}$ during the encoding of maximum span. Main effects of age (** : $p < 0.01$) and space (** : $p < 0.01$) are represented. **B)** ΔHHb during the encoding of maximum span. We represented differences between YA and OA in VWCT (* : $p < 0.05$), space effect for the OA group (* : $p < 0.05$) and the main effect of age on the right of the figure (* : $p < 0.05$). **C)** $\Delta\text{O}_2\text{Hb}$ during the encoding of failure span. Main effects of age (** : $p < 0.01$) and space (** : $p < 0.01$) are represented. **D)** ΔHHb during the encoding of failure span. We represented significant differences between YA and OA in VWCT (* : $p < 0.05$) and space effect for OA group (* : $p < 0.05$).

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Table 2

Correlations between raw scores in cognitive tests, VSWM tasks and oxygenation parameters in maximum span and failure span encoding.

Cognitive domain	Psychological tests	e-CBT		VWCT	
		r value	P value	r value	P value
Mental Rotation	MRT	0.64	<0.001	0.68	<0.001
Planning	ZOO	0.45	<0.001	0.34	<0.05
Attention. WM. Planning	REY R	0.60	<0.001	0.59	<0.001
Inhibition	STROOP I	-0.63	<0.001	-0.54	<0.001
Cognitive flexibility. Visuo-spatial exploring	TMT A	-0.54	<0.001	-0.49	<0.001
	TMT B	-0.40	<0.01	-0.33	<0.05
	Δ TMTs (B-A)	-0.28	<0.05	-0.21	0.116
Span level	Oxygenation parameters				
Maximum span	Δ O ₂ Hb	0.41	<0.01	0.29	<0.05
	Δ HHb	-0.15	0.26	-0.52	<0.01
Failure span	Δ O ₂ Hb	0.32	<0.05	0.31	<0.05
	Δ HHb	-0.11	0.43	-0.50	<0.001

r = correlation coefficient (Bravais-Pearson). Data written in bold show a significant relation between raw scores in cognitive tests and span score.

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Table 3

Regression analysis for the variables identified as correlated to VSWM tasks.

Variables	e-CBT (R = 0.81; R ² = 0.67)				VWCT (R = 0.80; R ² = 0.63)			
	B value	P value	95 % CI		B value	P value	95 % CI	
			Lower bound	Upper bound			Lower bound	Upper bound
Age	-0.3	<0.05	-0.023	0.014	0.1	0.280	-0.027	0.008
Level of education	0.1	0.324	-0.144	0.426	-0.01	0.871	-0.336	0.285
Sex	-0.2	0.235	-0.022	0.902	-0.1	0.271	-1.034	0.297
Δ HHb (failure span)					-0.2	<0.05	-0.322	-0.005
MRT	0.3	<0.01	0.045	0.223	0.4	<0.001	0.091	0.303
REY					0.3	<0.05	0.008	0.129
ZOO	0.2	<0.05	0.019	0.187				

B = regression coefficient, CI = confidence interval, R = correlation coefficient, R² = coefficient of determination. Data written in bold show a significant relation between raw scores in cognitive tests and span score.

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