1 **Spatial working memory in immersive virtual reality foraging: path organization,**

2 **traveling distance and search efficiency in humans (*Homo sapiens*)**

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5 Short title: Working memory in virtual reality foraging

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10   Abstract

11   Search and serial recall tasks were used in the present study to characterize the factors

12   affecting the ability of humans to keep track of a set of spatial locations while traveling

13   in an immersive virtual reality foraging environment. The first experiment required the

14   exhaustive exploration of a set of locations following a procedure previously used with

15   other primate and non-primate species to assess their sensitivity to the geometric

16   arrangement of foraging sites. The second experiment assessed the dependency of

17   search performance on search organization by requiring the participants to recall

18   specific trajectories throughout the foraging space. In the third experiment, the distance

19   between the foraging sites was manipulated in order to contrast the effects of

20   organization and traveling distance on recall accuracy. The results show that humans

21   benefit from the use of organized search patterns when attempting to monitor their

22   travel though either a clustered "patchy" space or a matrix of locations. Their ability to

23   recall a series of locations is dependent on whether the order in which they are explored

24   conformed or did not conform to specific organization principles. Moreover, the

25   relationship between search efficiency and search organization is not confounded by

26   effects of traveling distance. These results indicate that in humans, organizational

27   factors may play a large role in their ability to forage efficiently. The extent to which

28   such dependency may pertain to other primates and could be accounted for by visual

29   organization processes is discussed on the basis of previous studies focused on

30   perceptual grouping, search, and serial recall in non-human species.

31

32   Keywords: Working Memory; Spatial strategies; Primates; Virtual Reality.

Introduction

34 Working Memory (WM) enables the temporary storage of information needed to

35 support other cognitive functions and provides an interface for perception, long-term-

36 memory and action [Baddeley, 2003]. In studies of human cognition, the notion of WM

37 has a close relationship with that of general mental capacity [see Cowan 2005] and it

38 has been linked to attention, executive functions and the ability to integrate information

39 from different modalities [Baddeley, 1996]. Since WM capacity is related to higher

40 cognitive skills, its study in a comparative context may provide important information

41 concerning what is characteristic of human cognition and inform inferences about its

42 evolution throughout the primate order. Indeed, an expansion in WM capacity has been

43 recently considered as one of the main triggers of the emergence of human cognition

44 [Balter 2010; Coolidge & Wynn, 2005; Nowell, 2010; Welshon 2010; Wynn &

45 Coolidge 2010].

46   Spatial WM enables the temporary retention of locations and the non-verbal

47 nature of the tasks used to measure it makes it suitable for comparative studies. Spatial

48 WM has been assessed in children and animals with foraging-type tasks requiring the

49 exhaustive exploration of a set of baited containers placed in different locations within a

50 foraging space [e.g. MacDonald & Wilkie, 1990; MacDonald, Pang & Gibeault, 1994;

51 see De Lillo, 2012, for a review]. In these tasks, in any given trial subjects need to keep

52 track of the locations explored to avoid costly errors consisting in re-visiting containers

53 from which the reward has been collected. [See also Menzel, 2010; Sayers & Menzel,

54 2012].

55   Studies where the configuration of the containers has been systematically

56   manipulated [De Lillo, Visalberghi & Aversano, 1997; De Lillo, Aversano, Tuci &

57   Visalberghi, 1998] indicate that the structure of the search space and the paths chosen

58   by the subjects to explore it can have a strong effect on search efficiency. The

59   relationship between the geometry of foraging space, search organization, and search

60   efficiency is particularly evident in primates. For example, capuchin monkeys (*Cebus*

61   *apella*), the only non-human primate species tested so far using this paradigm, minimize

62   the number of errors they make when they explore containers arranged in spatial

63   clusters [De Lillo, Visalberghi & Aversano, 1997]. Moreover, in such a patchy search

64   space their search efficiency is correlated with the use of strategies, which involve

65   depleting all containers within a given cluster before moving on to another cluster [De

66   Lillo, Visalberghi & Aversano, 1997]. Some studies have suggested that this ability may

67   not pertain to non-primate species such as mice [Valsecchi, Bartolomucci, Aversano &

68   Visalberghi, 2000], rats [Foti, Mandolesi, Aversano & Petrosini, 2007] and tree-shrews

69   [Bartolomucci, de Biurrun & Fuchs, 2001].

70   It could be suggested that capuchin monkeys' ability to search efficiently in a

71   clustered arrangement could be an expression of a specific behavioural adaptation,

72   shared by several primate species, to forage on patchy resources [Milton, 1993]. A

73   greater memory capacity would be particularly useful to frugivores because it increases

74   foraging efficiency when searching for fruiting trees and, thus, it is a trait which would

75   have been selected for. Investigations using other search spaces affording systematic

76   searches, such as a circular arrangement of foraging sites, additionally highlight a

77   degree of flexibility in capuchin monkeys' ability to organize effective search strategies

78   as a function of the structure of the foraging space [De Lillo, Aversano, Tuci &

79   Visalberghi, 1998]. As such, this ability could be related to relatively high-level

80   cognitive functions that capuchin monkeys (and possibly other non-human primate

81   species yet to be tested) may share with humans. In order to assess this possibility, it is

82   important to obtain data on humans, tested under conditions similar to the enclosures or

83   semi-natural settings that can be used with other primates. However, it is not always

84   easy to find large environments where familiarity and other relevant variables, such as

85   the geometry of the environment and the layout of visual cues and landmarks, can be

86   easily controlled with adult humans. More importantly, although it is useful to sample

87   the search strategies which different organisms may spontaneously deploy in foraging,

88   this type of search task generally only affords correlational investigations of the

89   relationship between spatial strategies and WM performance. It is, therefore, difficult to

90   infer a causal relationship between these two variables using this methodology.

91   The experimental study of the relationship between the geometric arrangement

92   of spatial items, the patterns used to select them, and spatial WM has been carried-out

93   using Immediate Serial Spatial Recall (ISSR) tasks. These tasks are based on variations

94   of the Corsi test [Corsi, 1972], which, in its standard version, requires human

95   participants to reproduce sequences of finger taps on a wooden blocks irregularly

96   arranged on a tray. In computerized versions of this task, a set of identical icons are

97   displayed on a touch sensitive computer monitor. In the encoding phase, the icons flash,

98   or temporarily change color in turn, describing sequences of spatial locations, which the

99   participants have to reproduce in a recall phase by touching the icons in the correct

100 order on the screen. Using clustered arrays of locations it has been possible to show that

101 human ISSR is more accurate for patterns similar to those spontaneously deployed by

102 monkeys in similarly structured foraging environments [De Lillo, 2004; De Lillo &

103   Lesk, 2010; De Lillo, 2012]. Humans also benefit from spatial structure in ISSR tasks

104   where items are arranged as a square matrix. There, sequences with consecutive items

105   within the same row, column or diagonal are reproduced more accurately than

106   sequences violating this principle [Bor, Duncan, Wiseman & Owen, 2003].

107   In order to assess whether similarities or interspecies differences emerge

108   between humans and non-human primates in the ability to benefit from the detection

109   and use of similar constraints, Fagot and De Lillo [2011] have recently used a variation

110   of this ISSR task with baboons (*Papio papio*). Baboons engaged with the task and

111   proved competent in reporting back sequences of up to four items above chance. Such a

112   span is not very far from that suggested for immediate recall and general mental

113   capacity for unstructured material in humans [Cowan, 2001]. Nevertheless, the monkeys

114   did not seem to be able to benefit to the same degree as humans from sequences with

115   collinear consecutive items. While using a similar task with humans, an fMRI study

116   showed that such ability is dependent on functions of the dorso-lateral pre-frontal cortex

117   [Bor et al., 2003]. Therefore, it is possible that such ability may be related to the

118   expansion of the pre-frontal cortex that is particularly evident in humans [Fuster, 1989].

119   Although ISSR and foraging can provide complementary information regarding

120   the relationship between spatial structure, search organization, and memory

121   performance, there are important differences between these two types of tasks. ISSR is

122   typically assessed in much smaller environments and, crucially, ISSR tasks normally

123   offer a bird's eye view of search space not available to subjects walking throughout a

124   dispersed foraging environment. When an aerial view of the entire configuration of

125   items is continuously available to the subject throughout the task, the perception of

126   shapes generated by the presentation of the to-be-recalled sequences is likely to play a

127 role in their encoding. In fact, it has been suggested that the benefits of organized ISSR

128 patterns within a matrix of items derive from chunking them into visual *gestalten* [Bor

129 et al., 2003]. If that is the case, the diminished benefit for the recall of organized

130 patterns observed in baboons [Fagot & De Lillo, 2011] would be consistent with a large

131 body of literature now published on baboons [Fagot & Deruelle, 1997; Deruelle &

132 Fagot, 1997; 1998] and capuchin monkeys [Spinozzi, De Lillo & Truppa, 2003; De

133 Lillo, Spinozzi, Truppa & Naylor, 2005; De Lillo, Spinozzi, Palumbo & Giustino, 2011]

134 showing that monkeys may be less prone than humans to assemble local elements into

135 global shapes on the basis of the use of perceptual organization principles.

136   Differences between humans and other primates in the ability to use structure in

137 spatial tasks may thus be confined to visual perceptual abilities; albeit of possible high

138 level and dependent on top-down functions [see De Lillo et al., 2011, for a discussion].

139 The possibility that differences in this domain between humans and other primate

140 species could be entirely explained on the basis of their differences in perceptual

141 organization processes would be weakened by results showing that humans benefit from

142 the encoding of spatial structure in tasks where perceptual grouping processes are less

143 likely to take place. This would be the case of foraging tasks where the view point of

144 the subjects changes as they navigate throughout the environment and which do not

145 provide a bird's eye view of both the configuration of locations and of the path taken to

146 explore them. It is therefore important to assess effects of structure in foraging tasks

147 where the subject navigates through the environment with limited perceptual access to

148 the structure of the overall foraging space compared to typical ISSR tests.

149 We attempted to provide data that could be used to inform the issues discussed above by

150 using immersive virtual reality technology to test humans in a novel combination of

151   foraging and serial spatial recall. In our first experiment we used a virtual foraging task

152   to assess organizational principles spontaneously deployed by humans when they are

153   left free to explore foraging sites arranged in clusters or as a square matrix (see Figure 1

154   below). In the second experiment we used the same large immersive virtual foraging

155   environments to assess ISSR for navigational trajectories, which could conform to or

156   violate specific forms of serial-spatial structure. Finally in our third experiment we

157   manipulated the size of the foraging environment and the distance between the sites to

158   be recalled together with the serial order in which they had to be explored. This was

159   done to contrast the effect of path length and path structure on the ability to monitor

160   series of moves in the foraging space.

161

162   **Experiment 1**

163   **Methods**

164   All research carried out for this article adhered to the American Society of

165   Primatologists principles for the ethical treatment of primates and to all UK legal

166   requirements. This study received approval from the required institutional ethics

167   committee.

168   Eight female and two male human participants (N = 10, M age = 23.40 ± SD = 4.90

169   years, age range = 18-36 years) were tested in a Virtual Reality (VR) laboratory at the

170   School of Psychology, University of Leicester. Vizard 3.0 software enabled the

171   presentation of a virtual environment consisting of a set of 9 poles surmounted by a

172   white sphere within a large virtual hall with richly textured surfaces and a variety of

173   landmarks (as shown in Figure 1) via an NVIS nVisor stereoscopic head mounted

174   display. An Inter-Sense position tracker determined the viewpoint depending on the

175   head and body movement of the participants who operated a wand to navigate and

176   produce responses.

177   --------------

178   Figure 1

179   -------------

180   Depending on the condition, the poles were arranged as a 3 x 3 square matrix (Figure

181   1b) with an inter-pole distance of 2m or in clusters (Figure 1a), with an inter-pole

182   distance of 1m within a cluster and a minimum distance of 2m between poles located in

183   different clusters. In each trial, participants were required to select each of the 9 poles in

184   any order. A pole was selected by navigating towards it in the virtual environment,

185   placing a virtual hand visible within the display on the sphere surmounting the pole and

186   pulling the wand trigger. A brief message confirmed that the location had been "visited"

187   before participants traveled to another pole in the environment, but no cues were left to

188   mark visited locations. No physical walking movements were required on the part of

189   the participant throughout the task as traveling in the virtual environment was controlled

190   by moving a small joystick located on the wand with the thumb. The head movements

191   of the participant were tracked by the intersense system and used to update the view

192   point producing a vivid immersive experience. Performance was measured as the

193   average number of visit to poles. In any trial, optimal performance would be evidenced

194   by the use of 9 visits to search the set of poles. Visits in excess of this indicated errors

195   deriving from returning to poles already selected. Participants received 6 trials

196   alternating matrix and clusters with the configuration used for the starting trial

197   counterbalanced. The facing direction at the beginning of each trial was randomized

198   across trials, whilst the starting distance from the centre of the array was kept constant

199   at 7m.

200   **Results**

201   The average number of visits to poles was $9.07 \pm$ SD 0.20 in the clusters and $9.47 \pm$ SD

202   0.99 in the matrix condition. Unsurprisingly, considering the nearly optimal

203   performance in both conditions, the two means were not statistically different.

204   The trajectories followed in the clustered configuration always featured the exhaustive

205   exploration of a cluster before moving onto the next. On the single occasion where

206   errors occurred, they were due to a second exploration of all the items within a cluster

207   already visited. In all trials except one, when searching the matrix, subjects performed

208   consecutive visits to locations within the same row column or diagonal and all poles

209   within a line or column were exhaustively explored before moving to a pole in another

210   line or row. The single trial where this did not happen required 23 pole visits to

211   complete.

212   **Discussion**

213   Experiment 1 featured a search task similar to that presented in real-life search spaces

214   with other animals. De Lillo and co-workers [1997] tested capuchin monkeys in a task

215   requiring the exhaustive search of a set of containers, arranged either as a matrix or a

216   clustered configuration, to retrieve items of food. In subsequent studies, the task was

217   adapted for use with mice [Valsecchi et al., 2000], rats [Foti et al, 2007] and tree shrews

218   [Bartolomucci et al., 2001; see De Lillo, 2012, for a review]. In the present study, adult

219   humans were required to perform an exhaustive search of a set of nine poles and were

220   left free to select their own search trajectories throughout the foraging space. This type

221   of search task helps the identification of any search strategy which animals of different

222   species may develop in response to the spatial constraints afforded by the search space.

223   The efficacy of these different strategies can then be examined in relation to the ability

224   of the animals to monitor their moves within the foraging space in order to avoid

225   revisiting locations already depleted of food in any given trial.

226   Foraging tasks, where the subjects are left free to organize their search trajectory

227   through the sites to be visited, are extremely important in order to determine the

228   spontaneous emergence of search strategies in a particular species. Thus, it was

229   important to implement such a task with adult humans in Experiment 1. In fact, this was

230   the first time that adult humans have been tested in VR search environments featuring a

231   configuration of foraging sites similar to those used to test other primate and non-

232   primate animal species [Bartolomucci, de Biurrun & Fuchs, 2001; De Lillo et al., 1997;

233   De Lillo, 2012; Foti et al., 2007; Valsecchi, Bartolomucci & Aversano, 2000]. The

234   results indicated that humans spontaneously organized their searches deploying

235   trajectories which were consistent with those which would allow the reduction of the

236   memory load associated with the foraging task. Thus, they search a clustered space by

237   systematically exploring each cluster in turn. This is a strategy that would allow a

238   hierarchical representation of the search space resulting in a more economic storage of a

239   sequence of spatial locations [De Lillo et al., 1997; De Lillo, 2004; De Lillo & Lesk,

240   2010]. Such a strategy has been observed in capuchin monkeys [De Lillo et al., 1997]

241   and to a certain extent in tree shrews [Bartolomucci et al., 2001] but has been reported

242   to be absent in rats [Foti et al., 2007; De Lillo, 2012] and mice [Valsecchi et al., 2000].

243   When searching a matrix of locations, the trajectories followed by humans conformed to

244 the linear constraints of the configuration, a strategy also suggested to lead to a

245 reduction of the memory load of the task [De Lillo et al., 1998; Bor et al., 2003]. This

246 strategy has not been observed in any of the non-human animal species tested so far

247 [Bartolomucci et al. 2001; De Lillo et al., 1997; De Lillo, 2012; Foti et al., 2007;

248 Valsecchi et al., 2000]. The fact that there is a relationship between the use of organized

249 search trajectories and foraging performance in humans is suggested by the very few

250 trials where the above principles were violated, which were characterised by a larger

251 number of costly revisits to locations already explored. Nevertheless the correlational

252 nature of those observations and the rarity of these events do not make it possible to

253 infer a causal relationship between search organisation and performance in the same

254 way as it could be demonstrated by the experimental manipulation of search trajectories.

255 Albeit such manipulation is not possible with spontaneous search tasks, it is possible in

256 serial recall tasks specifically designed for this purpose (Bor et al., 2003; De Lillo,

257 2004; De Lillo & Lesk, 2010; De Lillo, 2012). Thus in Experiment 2, we used our VR

258 set-up in order to use for the first time a serial recall procedure in a three-dimensional

259 navigational environment.

260

261   **Experiment 2**

262 **Methods**

263 The same apparatus and the same virtual environments developed for Experiment 1

264 were used in Experiment 2. The same 10 participants took part in both experiments.

265 Experiment 2 took place 1 day after the completion of Experiment 1. The specific

266 procedures used in Experiment 2 are described below.

267   Experiment 2 featured a presentation and a recall phase. In the presentation phase, one

268   of the white spheres surmounting the poles turned red until the participant travelled

269   through the environment and selected it by operating the wand. A second pole would

270   then turn red until selected, and so on, until the 9 poles had been visited. The recall

271   phase then began. The starting position was reinstated and participants had to recall the

272   sequence of the presentation phase by navigating throughout the foraging space and by

273   selecting the poles in the same order. The spheres remained white at all times during

274   this phase.

275   Each trial featured either the clusters or the matrix configuration of poles and the to-be-

276   recalled sequences could either be structured or unstructured. Structured sequences in

277   the clustered condition featured consecutive items within the same cluster until the

278   cluster was exhaustively explored; unstructured sequences always had consecutive

279   items in different clusters. Following Bor et al. [2003], structured sequences in the

280   matrix condition had consecutive items within the same row, column or diagonal,

281   whereas non-structured sequences always violated this constraint. Participants received,

282   in random order, 6 trials for each condition according to a 2 (configuration:

283   clusters/matrix) x 2 (structure: structured/unstructured) repeated measure design.

284

285   **Results**

286   All the statistical analyses described below use a two-tailed P value.

287   Figure 2 shows the proportion of poles selected in the correct order in the four

288   conditions of Experiment 2. A 2 (configuration) x 2 (structure) ANOVA carried out on

289   these values showed a higher level of recall in structured sequences, $F = 38.88$, $df = (1,$

290   9), P < 0.001, $\eta_p^2 = 0.81$. Neither the effect of configuration nor the interaction structure

291   by configuration proved significant.

292   ------------

293   Figure 2

294   ------------

295   A time analysis provided converging results. The mean response time (RT) for

296   correctly selected poles in each condition is presented Figure 3.

297   -----------

298   Figure 3

299   -----------

300   The same ANOVA carried out on these values revealed faster RT for structured

301   sequences, F = 48.87, df = (1, 9), P < 0.001, $\eta_p^2 = 0.85$, but no effects of configuration

302   or interactions.

303   **Discussion**

304   In experiment 2 we implemented a serial recall task in a foraging environment. The

305   results clarify that there is a dependency between organizational principles and spatial

306   WM in humans under these testing conditions. Benefits of spatial structure in humans

307   have been observed in ISSR tasks [Bor et al., 2003; De Lillo, 2004; De Lillo & Lesk,

308   2010] where the configuration of items is laid out in front of the observer and shown to

309   play an important role in sequence encoding [Avons, 2007]. The results of this

310   experiment indicate that the benefits of organization are also evident when people

311   navigate through the set of locations in a large virtual foraging environment.

312   The size of the environment and the immersive VR set-up required the subjects to

313   navigate through the environment in a way that determined a continuous change of

314   perspective and view-point at any point of the exploration of the set or during recall.

315   This made it possible to determine for the first time that effects of structure in spatial

316   recall are not confined to situations affording a bird's eye view of the configuration

317   explored at any point during the task. However, in the task featured in Experiment 2 the

318   length of the search path was not entirely independent from the degree of structure. In

319   fact, in structured sequences the path length was often shorter than in non-structured

320   sequences. There are several reasons for suspecting that path length may affect recall so

321   that a shorter path length should be associated with better memory recall. The first is

322   that this effect has been observed in small scale spatial serial recall tasks where

323   participants use finger movements to tap on locations presented on a computer monitors

324   in a given order [Parmentier, Elford & Maybery, 2005]. Moreover, if we assume that

325   shorter movements require typically less time to perform, a better recall of sequences

326   characterized by a shorter path may be expected on the basis of working-memory

327   models which assume a relationship between the time it takes to rehearse a sequence

328   and its recall [see Smyth & Scholey, 1994, for a discussion of this point]. It was,

329   therefore, important to assess if the length of the path used by the participants to explore

330   the to-be-recalled locations in the present task affected accuracy and potentially

331   confounded the results of Experiment 2. In order to assess this possibility, in

332   Experiment 3 we dissociated path length and organization by manipulating the distance

333   between the to-be-explored sites as well as the structure of the search path.

334

335   **Experiment 3**

336   **Methods**

337   A new set of participants took part in Experiment 3. They were eight male and eight

338   female psychology undergraduate students from the University of Leicester (N = 16, M

339   age = 21.13 ± SD 2.88 years, age range: 18-27) who received course credits for their

340   participation. The general task was the same as that used in Experiment 2. However, the

341   design of Experiment 3 featured the inter-pole distance as a further variable, which was

342   manipulated by changing the scale of the search environment while keeping the size of

343   the poles and the objects in the environment constant. There were a long and a short

344   inter-pole distance conditions. They will be referred to as long-path and short-path

345   conditions hereafter, since they were used to affect the length of the path taken by the

346   subjects in any particular trial. The inter-pole distance in the long-path condition was

347   made three times as long as the short-path condition. In particular, the minimum

348   possible distance between the poles was 2.1m in the long-path condition and 0.7m in the

349   short-path condition. The starting distance from the centre of the array of poles in the

350   long-path condition was 14.7m and 4.9m in the short path condition. Figure 4 shows the

351   two configurations and display sizes.

352   ------------

353   Figure 4

354   ------------

355 The inter-pole distances used in the short-path condition and in the long-path condition

356 were calculated so that the long-path structured trials required walking a longer distance

357 through the VR environment than in the short-path unstructured trials. Thus, for

358 Experiment 3 a 2 (configuration: cluster/matrix) x 2 (structure: structured/unstructured)

359 x 2 (inter-pole distance: short-path/long-path) repeated measure design was used.

360 As in Experiment 2, in each trial participants completed the presentation phase

361 where they were required to navigate towards the pole which turned red and select it,

362 until a sequence of visits to all nine poles was accomplished. Then a recall phase

363 ensued, which required the participants to navigate throughout the environment to visit

364 the poles in the same order. Participants received alternating trials of the short-path and

365 long-path condition, with the starting condition randomized across participants. Apart

366 from this constraint, the conditions were randomized across trials. Each participant

367 received two trials per condition for a total of 16 trials. Participants were given a short

368 break every two trials or when required and a ten minute break after eight trials. The

369 definition of structure was the same as used in Experiment 2. The relative distance

370 between poles in the cluster and the matrix condition was also the same as in

371 Experiment 2.

372 **Results**

373 The proportion of items correctly recalled in the clustered condition is shown in Fig. 5a,

374 and in the matrix condition in Fig. 5b.

375 ------------

376 Figure 5

377   ------------

378   A 2 (path length) x 2 (configuration) x 2 (structure) ANOVA carried out on the

379   proportion of items correctly recalled showed a significant effect for structure, $F = 7.11$,

380   df = (1, 15), $P < 0.05$, $\eta_p^2 = 0.32$, supporting the results of Experiment 2. However, the

381   effects for path length, $F = 3.55$, df = (1, 15), $P = 0.08$, $\eta_p^2 = 0.19$, and configuration, F

382     $= 0.08$, df = (1 15), $P = 0.79$, $\eta_p^2 = 0.01$, were not significant. A paired-samples t-test

383   was used to carry out the critical comparison between recall accuracy observed for

384   short-path length unstructured trials and long-path structured trials, for both matrix and

385   clusters. The t-tests showed that for the clustered array, structured sequences in the

386   long-path condition (M = 0.76 ± SD 0.16) were recalled with a higher level of accuracy

387   than unstructured sequences with a short-path length (M = 0.56 ± SD 0.30), $t = 4.00$, df

388   = 15, $P < 0.05$. This demonstrates that structured sequences are easier to recall than

389   unstructured sequences, even when their path-length is longer. In the matrix condition,

390   the comparison between the recall accuracy for structured sequences with a long path

391   (M = 0.64 ± SD 0.32) and unstructured sequences with a short path (M = 0.59 ± SD

392   0.29) was not significant, $t = 0.67$, df = 15, $P = 0.51$.

393   As in Experiment 2, we carried out a time analysis that was based on correct responses

394   only. One participant did not recall correctly any item in the clustered short path

395   unstructured condition. For this reason, there are 14 degrees of freedom for the error in

396   the analyses reported below. For all poles selected in the correct order, the response

397   times were obtained by averaging the means of the median response time observed in

398   trials of each condition. These values are shown in Fig. 6a and 6b for the clustered and

399   the matrix condition, respectively.

400   ----------

401   Figure 6

402   ----------

403   A 2 (path-length) x 2 (configuration) x 2 (structure) ANOVA carried out on these

404   values showed significant main effects of path-length between the poles, $F = 127.73$, df

405    $= (1, 14)$, $P < 0.001$, $\eta_p^2 = 0.90$, configuration of the poles, $F = 7.05$, df $= (1, 14)$, $P <$

406   0.05, $\eta_p^2 = 0.34$, and structure of the to-be-recalled sequence, $F = 35.86$, df $= (1, 14)$, P

407   < 0.001, $\eta_p^2 = 0.72$. A significant interaction configuration by structure was also

408   revealed, $F = 10.22$, df $= (1, 14)$, $P < 0.05$, $\eta_p^2 = 0.42$. A paired samples t-test showed

409   that for the long path condition with the matrix configuration, there was no significant

410   difference in time taken to recall sequences between unstructured ($M = 13.42 \pm$ SD

411   3.83) and structured sequences ($M = 11.71 \pm$ SD 4.83), $t = -1.79$, df $= 15$, $P = 0.09$. In

412   the short-path condition however, unstructured sequences ($M = 6.79 \pm$ SD 2.02) took

413   significantly longer to recall than structured ($M = 5.45 \pm$ SD 1.86), $t = -3.14$, df $= 15$, P

414   < 0.05. For the long path condition in the clustered configuration, the unstructured

415   sequences ($M = 13.72 \pm$ SD 5.15) took significantly longer to recall than structured

416   sequences ($M = 7.23 \pm$ SD 2.00), $t = -6.03$, df $= 15$, $P < 0.001$. The same pattern was

417   observed in the short path conditions for the clustered configuration (unstructured, $M =$

418    $7.83 \pm$ SD 3.93, and structured, $M = 4.25 \pm$ SD 1.27, $t = -3.80$, df $= 14$, $P < 0.05$).

419   The comparison of long-path structured and short-path unstructured condition for both

420   the matrix and clusters showed that the long-path structured sequences for the matrix

421   took significantly longer to recall than then the short-path unstructured matrix, $t = 4.84$,

422   df $= 15$, $P < 0.001$. There was no significant difference however in the clustered

423   configuration between the long path structured condition and the short path unstructured

424   condition, t = -0.97, df = 14, P = 0.35.

425   **Discussion**

426   The length of the movement path necessary to reproduce a sequence of responses in a

427   small scale spatial array of locations, such as that used in variations of the Corsi test,

428   has been shown to have an effect on spatial recall in humans [Parmentier et al., 2004].

429   Fagot and De Lillo [2011], observed a negative effect of path length in baboons tested

430   in one of the first implementation of variation of the Corsi test in non-human primates.

431   It was, therefore, important to address the potential confounding effects of path length

432   and use of spatial structure in the present study where they could have been present or

433   even exacerbated in a task requiring virtual navigation in a larger search space. In

434   Experiment 3 we tested the effect of path length with both the clustered and the matrix

435   configuration. We compared the recall of structured and unstructured sequences

436   characterized by a long or a short path length. Importantly, we ensured that the

437   structured sequences in the large arrays had a longer path length than the unstructured

438   sequences in the small array. The results strongly suggest that path length cannot in

439   itself explain the beneficial effects of path structure observed in Experiment 2. In fact,

440   in the clustered configuration a more accurate recall was observed for structured

441   sequences even when these had a longer path length than unstructured sequences. In the

442   matrix condition, we observed a difference between these two critical conditions, which

443   was in the same direction but did not reach statistical significance. The time analysis

444   confirmed that the pattern of results obtained for recall accuracy in the two critical

445   conditions could not be explained on the basis of the time it took on average to select

446   consecutive items. In fact, in the matrix array a longer median RT was observed in the

447 long-structured condition compared to the short-unstructured condition. Yet these two

448 conditions did not differ in recall accuracy. In the clustered array, similar RTs were

449 observed in the long-structured condition and in the short-unstructured condition. Yet

450 the recall accuracy in the former was higher than in the latter.

451

452 **General Discussion**

453 In the present study, we carried out a series of three experiments with adult humans

454 using immersive virtual reality foraging environments. The use of this technology

455 allowed us to obtain information about human spatial WM that can be used in a

456 comparative context. Moreover, immersive VR made it possible for the first time to

457 implement a serial recall task within a foraging space. Serial recall enabled us to gain

458 important additional information concerning the relationship between the use of

459 organized paths throughout a search space and memory.

460 In the first instance, the results of the present study indicate that in a "patchy" foraging

461 environment such as our clustered configuration humans spontaneously deploy a search

462 strategy similar to that shown by capuchin monkeys [De Lillo et al., 1997], the only

463 non-human primate species tested so far in such a task. This strategy is best defined as

464 "clustering" and involves searching all the locations within a cluster before moving on

465 to searching locations within another cluster. A similar tendency had been previously

466 observed in 4-year old children tested in a real-life task analogous to that presented to

467 the capuchin monkeys [De Lillo, 2012]. The fact that a similar strategy emerges in both

468 species in the virtual reality task seem to indicate that overall the VR was capturing

469 essential aspects of the real life task.

470   In most tropical forest environments, food resources are distributed patchily in

471   time and space. When given the opportunity to search food locations, macaques have

472   been found to use the distribution of previously found food to anticipate further

473   locations, an ability which would increase natural foraging success and efficiency

474   [Hemmi & Menzel, 1995]. The ability to search efficiently in a patchy foraging space

475   could be the expression of a specific adaptation shared by most primate species to recall

476   and relocate patchy resources such as fruiting trees and this may have played a critical

477   role in the evolution of primate cognitive abilities [Milton, 1993; Zuberbühler &

478   Janmaat, 2010; see also Garber and Porter, this issue]. Elsewhere [De Lillo et al., 1998],

479   we have shown that capuchin monkeys are able to develop search strategies that enable

480   them to exploit resources distributed in a variety of spatial arrangements and argued that

481   they show a flexibility that seems to transcend the specific ability to benefit from a

482   patchy distribution of food resources. Nevertheless, capuchin monkeys do not seem to

483   be able to impose structure on a more diffuse foraging space such as a matrix of

484   locations and do not fully exploit the linear constraints afforded by such a search space.

485   The results of the present study show that humans are able to do so and as such seem to

486   have a higher degree of flexibility in detecting and exploiting items distributed across a

487   larger variety of search spaces. In fact, in contrast with capuchin monkeys, humans were

488   extremely principled and proficient with an arrangement of locations configured as a

489   square matrix. These results obtained in a free search task would be consistent with

490   those showing a remarkable ability of humans to benefit from the constraints imposed

491   by the linear organization of a matrix in serial recall tasks [Bor et al., 2003].

492   We have recently reported a difference between humans and baboons (*Papio*

493   *papio*) in the serial recall of items presented in locations defined by a virtual 5 x 5

494   square matrix on a computer monitor [Fagot & De Lillo, 2011]. Sequence structure and

495   path length were manipulated in the same study. Humans proved to be particularly

496   sensitive to structure as they recalled better sequences segmented according to the linear

497   structure of the matrix but they were not sensitive to path length. In contrast, baboons'

498   serial recall was not affected by the structure of the sequences but improved for

499   sequences with a shorter path length [Fagot & De Lillo, 2011]. In common with other

500   traditional serial recall tasks, such as the Corsi test presented on computer monitors, the

501   task used by Fagot and De Lillo [2011] offered a bird's eye view of the spatial

502   arrangement of the target locations and each of the locations to be selected was visible

503   at all time during both the presentation of the sequence and its recall. As such, the

504   ability to detect structural properties of the paths that had to be reproduced could rely on

505   perceptual organization. In fact, it has been proposed that greater recall of sequences

506   segregated by the linear organization of the set is due to forms of chunking based on

507   perceptual grouping [Bor at al., 2003].

508   There is now a rich set of results obtained with capuchin monkeys, baboons, and

509   humans that indicates important differences in the visual cognition of monkeys and

510   humans in their readiness to perceive the global spatial organization of a collection of

511   local elements [e.g. Fagot & Deruelle, 1997; Deruelle & Fagot, 1997; 1998; Spinozzi et

512   al., 2003; De Lillo et al., 2005; 2011]. In some cases, differences have been identified in

513   the readiness of humans and monkeys to use specific perceptual grouping cues [Fagot &

514   Deruelle, 1997; Parron & Fagot, 2007; Spinozzi, De Lillo & Castelli, 2004; Spinozzi,

515   De Lillo, Truppa & Castorina, 2009]. Therefore, when ISSR tasks afford an aerial view

516   of the array of locations differences between humans and monkeys could be reduced, in

517   principle, to interspecies differences in perceptual grouping.

518   The current experiments provide important information concerning this point. They

519   were carried out using serial recall in an immersive virtual reality environment that, as

520   in a real-life foraging task in navigational space, afforded a continuous change of

521   viewpoint during search or recall. Thus they clarify that humans are able to impose

522   strategies that allow them to benefit from spatial structure in a task where the

523   contribution of visual perceptual grouping processes is less obvious. If it was used in the

524   present task, a bird's eye representation of the configuration of the search space would

525   have needed to be actively constructed by the subjects on the basis of local view-points

526   experienced through navigation. The exact nature of the memory code used to benefit

527   from structure in humans cannot be evinced from the present results and it is a matter of

528   further investigation.

529   Spatial structuring in a foraging space may be based on the formation of a mental image

530   of the search space. It is possible that given the similarity of mental processes involved

531   in visual perception and visual imagery postulated by some theories [e.g. Borst &

532   Kosslyn, 2008; Kosslyn & Thompson, 2003], processes similar to perceptual grouping

533   acting on mental images of the search space may still pertain to the explanation of

534   effects of structure in our task. Monkeys seem to show similar patterns to humans in

535   experiments on mental rotation which suggest that they may have the capability for

536   mental imagery [Vauclair, Fagot & Hopkins, 1993] and have the ability to modulate the

537   perception of global spatial configurations of stimuli using top-down attentional

538   processes [De Lillo et al., 2011]. As such they could in principle show effects similar to

539   some of those observed here in humans. The comparative investigation of the extent to

540   which humans and monkeys structure mental images in a similar way would be a topic

541   of extreme interest. It could clarify whether differences in the ability to benefit from

542 linear structures between humans and monkeys extend beyond visual organization to

543 forms of memory coding of spatial information. This may have important implications

544 for our understanding of the extent in which monkeys represent a good model of human

545 non-verbal memory and cognition and of what could be uniquely human in this domain.

546

553

Authors' note

555 CDL designed the experiments, analysed the data and wrote the article. MK ran

556 Experiment 3, analysed the data and wrote the article. FCJ ran Experiments 1 and 2 and

557 contributed to the data analysis as part of a Nuffield Foundation undergraduate research

558 bursary.

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673

674   **Figure captions**

675   **Figure 1**. Examples of views of the VR foraging space: a) clusters, b) matrix. Apart

676   from the arrangement of poles the environment was the same in both conditions.

677   **Figure 2.** Proportion of poles selected in the correct order in each condition of

678   Experiment 2 and Error bars = 1 SE.

679   **Figure 3.** Response time (RT) recorded in each condition of Experiment 2. Error bars =

680   1 SE.

681   **Figure 4**. Screen-shots of VR environments used in Experiment 3. Top row: large

682   environments with long inter-pole and starting distance used for the long-path cluster

683   (left) and matrix (right) conditions. Bottom row: small environments with short inter-

684   pole and starting distance used for the short-path clustered (left) and matrix (right)

685   conditions. See text for full explanations and measurements.

686   **Figure 5.** Proportion of items correctly recalled in the clustered long and short-path

687   conditions (a), and in the matrix long and short-path conditions (b) of Experiment 3.

688   Error bars = 1 SE.

689   **Figure 6.** Response time (RT) recorded in the clustered long and short-path conditions

690   (a), and in the matrix long and short-path conditions (b) of Experiment 3. Error bars = 1

691   SE.