

RESEARCH ARTICLE

Spatial Working Memory in Immersive Virtual Reality Foraging: Path Organization, Traveling Distance and Search Efficiency in Humans (*Homo sapiens*)

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Search and serial recall tasks were used in the present study to characterize the factors affecting the ability of humans to keep track of a set of spatial locations while traveling in an immersive virtual reality foraging environment. The first experiment required the exhaustive exploration of a set of locations following a procedure previously used with other primate and non-primate species to assess their sensitivity to the geometric arrangement of foraging sites. The second experiment assessed the dependency of search performance on search organization by requiring the participants to recall specific trajectories throughout the foraging space. In the third experiment, the distance between the foraging sites was manipulated in order to contrast the effects of organization and traveling distance on recall accuracy. The results show that humans benefit from the use of organized search patterns when attempting to monitor their travel though either a clustered “patchy” space or a matrix of locations. Their ability to recall a series of locations is dependent on whether the order in which they are explored conformed or did not conform to specific organization principles. Moreover, the relationship between search efficiency and search organization is not confounded by effects of traveling distance. These results indicate that in humans, organizational factors may play a large role in their ability to forage efficiently. The extent to which such dependency may pertain to other primates and could be accounted for by visual organization processes is discussed on the basis of previous studies focused on perceptual grouping, search, and serial recall in non-human species. *Am. J. Primatol.* 76:436–446, 2014. © 2013 Wiley Periodicals, Inc.

Key words: working memory; spatial strategies; primates; virtual reality

INTRODUCTION

Working memory (WM) enables the temporary storage of information needed to support other cognitive functions and provides an interface for perception, long-term memory and action [Baddeley, 2003]. In studies of human cognition, the notion of WM has a close relationship with that of general mental capacity [see Cowan, 2005] and it has been linked to attention, executive functions and the ability to integrate information from different modalities [Baddeley, 1996]. Since WM capacity is related to higher cognitive skills, its study in a comparative context may provide important information concerning what is characteristic of human cognition and inform inferences about its evolution throughout the primate order. Indeed, an expansion in WM capacity has been recently considered as one of the main triggers of the emergence of human cognition [Balter, 2010; Coolidge & Wynn, 2005; Nowall, 2010; Welshon, 2010; Wynne & Coolidge, 2010].

Spatial WM enables the temporary retention of locations and the non-verbal nature of the tasks used

to measure it makes it suitable for comparative studies. Spatial WM has been assessed in children and animals with foraging-type tasks requiring the exhaustive exploration of a set of baited containers placed in different locations within a foraging space [e.g. MacDonald & Wilkie, 1990; MacDonald et al., 1994; see De Lillo, 2012, for a review]. In these tasks, in any given trial subjects need to keep track of

Contract grant sponsor: Capital Investment Fund; contract grant sponsor: Nuffield Foundation; contract grant number: URB/39517.

Conflicts of interest: None.

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Received 11 April 2013; revised 9 July 2013; revision accepted 29 July 2013

DOI: 10.1002/ajp.22195

Published online 3 September 2013 in Wiley Online Library (wileyonlinelibrary.com).

the locations explored to avoid costly errors consisting in revisiting containers from which the reward has been collected [see also Menzel, 2010; Sayers & Menzel, 2012].

Studies where the configuration of the containers has been systematically manipulated [De Lillo et al., 1997, 1998] indicate that the structure of the search space and the paths chosen by the subjects to explore it can have a strong effect on search efficiency. The relationship between the geometry of foraging space, search organization, and search efficiency is particularly evident in primates. For example, capuchin monkeys (*Cebus apella*), the only non-human primate species tested so far using this paradigm, minimize the number of errors they make when they explore containers arranged in spatial clusters [De Lillo et al., 1997]. Moreover, in such a patchy search space their search efficiency is correlated with the use of strategies, which involve depleting all containers within a given cluster before moving on to another cluster [De Lillo et al., 1997]. Some studies have suggested that this ability may not pertain to non-primate species such as mice [Valsecchi et al., 2000], rats [Foti et al., 2007], and tree shrews [Bartolomucci et al., 2001].

It could be suggested that capuchin monkeys' ability to search efficiently in a clustered arrangement could be an expression of a specific behavioral adaptation, shared by several primate species, to forage on patchy resources [Milton, 1993]. A greater memory capacity would be particularly useful to frugivores because it increases foraging efficiency when searching for fruiting trees and, thus, it is a trait which would have been selected for. Investigations using other search spaces affording systematic searches, such as a circular arrangement of foraging sites, additionally highlight a degree of flexibility in capuchin monkeys' ability to organize effective search strategies as a function of the structure of the foraging space [De Lillo et al., 1998]. As such, this ability could be related to relatively high-level cognitive functions that capuchin monkeys (and possibly other non-human primate species yet to be tested) may share with humans. In order to assess this possibility, it is important to obtain data on humans, tested under conditions similar to the enclosures or semi-natural settings that can be used with other primates. However, it is not always easy to find large environments where familiarity and other relevant variables, such as the geometry of the environment and the layout of visual cues and landmarks, can be easily controlled with adult humans. More importantly, although it is useful to sample the search strategies which different organisms may spontaneously deploy in foraging, this type of search task generally only affords correlational investigations of the relationship between spatial strategies and WM performance. It is, therefore,

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

The experimental study of the relationship between the geometric arrangement of spatial items, the patterns used to select them, and spatial WM has been carried out using immediate serial spatial recall (ISSR) tasks. These tasks are based on variations of the Corsi test [Corsi, 1972], which, in its standard version, requires human participants to reproduce sequences of finger taps on a wooden blocks irregularly arranged on a tray. In computerized versions of this task, a set of identical icons are displayed on a touch sensitive computer monitor. In the encoding phase, the icons flash, or temporarily change color in turn, describing sequences of spatial locations, which the participants have to reproduce in a recall phase by touching the icons in the correct order on the screen. Using clustered arrays of locations it has been possible to show that human ISSR is more accurate for patterns similar to those spontaneously deployed by monkeys in similarly structured foraging environments [De Lillo, 2004, 2012; De Lillo & Lesk, 2010]. Humans also benefit from spatial structure in ISSR tasks where items are arranged as a square matrix. There, sequences with consecutive items within the same row, column, or diagonal are reproduced more accurately than sequences violating this principle [Bor et al., 2003].

In order to assess whether similarities or interspecies differences emerge between humans and non-human primates in the ability to benefit from the detection and use of similar constraints, Fagot and De Lillo [2011] have recently used a variation of this ISSR task with baboons (*Papio papio*). Baboons engaged with the task and proved competent in reporting back sequences of up to four items above chance. Such a span is not very far from that suggested for immediate recall and general mental capacity for unstructured material in humans [Cowan, 2001]. Nevertheless, the monkeys did not seem to be able to benefit to the same degree as humans from sequences with collinear consecutive items. While using a similar task with humans, an fMRI study showed that such ability is dependent on functions of the dorso-lateral pre-frontal cortex [Bor et al., 2003]. Therefore, it is possible that such ability may be related to the expansion of the pre-frontal cortex that is particularly evident in humans [Fuster, 1989].

Although ISSR and foraging can provide complementary information regarding the relationship between spatial structure, search organization, and memory performance, there are important differences between these two types of tasks. ISSR is typically assessed in much smaller environments and, crucially, ISSR tasks normally offer a bird's eye view of search space not available to subjects walking throughout a dispersed foraging environment. When an aerial view of the entire configuration of items is

continuously available to the subject throughout the task, the perception of shapes generated by the presentation of the to-be-recalled sequences is likely to play a role in their encoding. In fact, it has been suggested that the benefits of organized ISSR patterns within a matrix of items derive from chunking them into visual *gestalten* [Bor et al., 2003]. If that is the case, the diminished benefit for the recall of organized patterns observed in baboons [Fagot & De Lillo, 2011] would be consistent with a large body of literature now published on baboons [Fagot & Deruelle, 1997; Deruelle & Fagot, 1997, 1998] and capuchin monkeys [Spinozzi et al., 2003; De Lillo et al., 2005, 2011] showing that monkeys may be less prone than humans to assemble local elements into global shapes on the basis of the use of perceptual organization principles.

Differences between humans and other primates in the ability to use structure in spatial tasks may thus be confined to visual perceptual abilities; albeit of possible high level and dependent on top-down functions [see De Lillo et al., 2011, for a discussion]. The possibility that differences in this domain between humans and other primate species could be entirely explained on the basis of their differences in perceptual organization processes would be weakened by results showing that humans benefit from the encoding of spatial structure in tasks where perceptual grouping processes are less likely to take place. This would be the case of foraging tasks where the view-point of the subjects changes as they navigate throughout the environment and which do not provide a bird's eye view of both the configuration of locations and of the path taken to explore them. It is therefore important to assess effects of structure in foraging tasks where the subject navigates through the environment with limited perceptual access to the structure of the overall foraging space compared to typical ISSR tests.

We attempted to provide data that could be used to inform the issues discussed above by using immersive virtual reality technology to test humans in a novel combination of foraging and serial spatial recall. In our first experiment we used a virtual foraging task to assess organizational principles spontaneously deployed by humans when they are left free to explore foraging sites arranged in clusters or as a square matrix (see Fig. 1 below). In the second experiment we used the same large immersive virtual foraging environments to assess ISSR for navigational trajectories, which could conform to or violate specific forms of serial-spatial structure. Finally in our third experiment we manipulated the size of the foraging environment and the distance between the sites to be recalled together with the serial order in which they had to be explored. This was done to contrast the effect of path length and path structure on the ability to monitor series of moves in the foraging space.

EXPERIMENT 1

Methods

All research carried out for this article adhered to the American Society of Primatologists principles for the ethical treatment of primates and to all UK legal requirements. This study received approval from the required institutional ethics committee.

Eight female and two male human participants ($N = 10$, M age = $23.40 \pm SD = 4.90$ years, age range = 18–36 years) were tested in a virtual reality (VR) laboratory at the School of Psychology, University of Leicester. Vizard 3.0 software enabled the presentation of a virtual environment consisting of a set of nine poles surmounted by a white sphere within a large virtual hall with richly textured surfaces and a variety of landmarks (as shown in Fig. 1) via an NVIS nVisor stereoscopic head mounted display. An InterSense position tracker determined the viewpoint

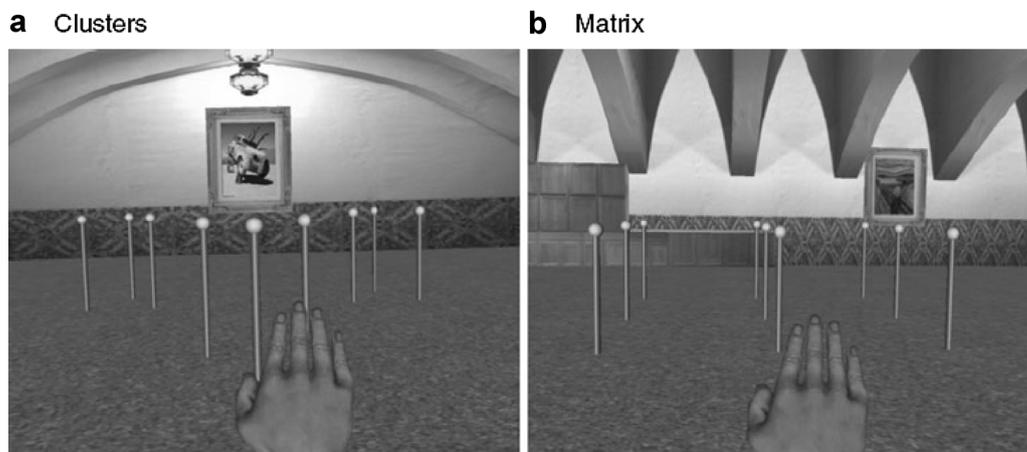


Fig. 1. Examples of views of the VR foraging space: (a) clusters and (b) matrix. Apart from the arrangement of poles the environment was the same in both conditions.

depending on the head and body movement of the participants who operated a wand to navigate and produce responses.

Depending on the condition, the poles were arranged as a 3×3 square matrix (Fig. 1b) with an inter-pole distance of 2 m or in clusters (Fig. 1a), with an inter-pole distance of 1 m within a cluster and a minimum distance of 2 m between poles located in different clusters. In each trial, participants were required to select each of the nine poles in any order. A pole was selected by navigating towards it in the virtual environment, placing a virtual hand visible within the display on the sphere surmounting the pole and pulling the wand trigger. A brief message confirmed that the location had been “visited” before participants traveled to another pole in the environment, but no cues were left to mark visited locations. No physical walking movements were required on the part of the participant throughout the task as traveling in the virtual environment was controlled by moving a small joystick located on the wand with the thumb. The head movements of the participant were tracked by the intersense system and used to update the view-point producing a vivid immersive experience. Performance was measured as the average number of visit to poles. In any trial, optimal performance would be evidenced by the use of nine visits to search the set of poles. Visits in excess of this indicated errors deriving from returning to poles already selected. Participants received six trials alternating matrix and clusters with the configuration used for the starting trial counterbalanced. The facing direction at the beginning of each trial was randomized across trials, while the starting distance from the centre of the array was kept constant at 7 m.

Results

The average number of visits to poles was $9.07 \pm \text{SD } 0.20$ in the clusters and $9.47 \pm \text{SD } 0.99$ in the matrix condition. Unsurprisingly, considering the nearly optimal performance in both conditions, the two means were not statistically different.

The trajectories followed in the clustered configuration always featured the exhaustive exploration of a cluster before moving onto the next. On the single occasion where errors occurred, they were due to a second exploration of all the items within a cluster already visited. In all trials except one, when searching the matrix, subjects performed consecutive visits to locations within the same row column or diagonal and all poles within a line or column were exhaustively explored before moving to a pole in another line or row. The single trial where this did not happen required 23 pole visits to complete.

Discussion

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

animals. De Lillo et al. [1997] tested capuchin monkeys in a task requiring the exhaustive search of a set of containers, arranged either as a matrix or a clustered configuration, to retrieve items of food. In subsequent studies, the task was adapted for use with mice [Valsecchi et al., 2000], rats [Foti et al., 2007], and tree shrews [Bartolomucci et al., 2001; see De Lillo, 2012, for a review]. In the present study, adult humans were required to perform an exhaustive search of a set of nine poles and were left free to select their own search trajectories throughout the foraging space. This type of search task helps the identification of any search strategy which animals of different species may develop in response to the spatial constraints afforded by the search space. The efficacy of these different strategies can then be examined in relation to the ability of the animals to monitor their moves within the foraging space in order to avoid revisiting locations already depleted of food in any given trial.

Foraging tasks, where the subjects are left free to organize their search trajectory through the sites to be visited, are extremely important in order to determine the spontaneous emergence of search strategies in a particular species. Thus, it was important to implement such a task with adult humans in Experiment 1. In fact, this was the first time that adult humans have been tested in VR search environments featuring a configuration of foraging sites similar to those used to test other primate and non-primate animal species [Bartolomucci et al., 2001; De Lillo, 2012; De Lillo et al., 1997; Foti et al., 2007; Valsecchi et al., 2000]. The results indicated that humans spontaneously organized their searches deploying trajectories which were consistent with those which would allow the reduction of the memory load associated with the foraging task. Thus, they search a clustered space by systematically exploring each cluster in turn. This is a strategy that would allow a hierarchical representation of the search space resulting in a more economic storage of a sequence of spatial locations [De Lillo, 2004; De Lillo & Lesk, 2010; De Lillo et al., 1997]. Such a strategy has been observed in capuchin monkeys [De Lillo et al., 1997] and to a certain extent in tree shrews [Bartolomucci et al., 2001] but has been reported to be absent in rats [De Lillo, 2012; Foti et al., 2007] and mice [Valsecchi et al., 2000]. When searching a matrix of locations, the trajectories followed by humans conformed to the linear constraints of the configuration, a strategy also suggested to lead to a reduction of the memory load of the task [Bor et al., 2003; De Lillo et al., 1998]. This strategy has not been observed in any of the non-human animal species tested so far [Bartolomucci et al., 2001; De Lillo, 2012; De Lillo et al., 1997; Foti et al., 2007; Valsecchi et al., 2000]. The fact that there is a relationship between the use

of organized search trajectories and foraging performance in humans is suggested by the very few trials where the above principles were violated, which were characterized by a larger number of costly revisits to locations already explored. Nevertheless the correlational nature of those observations and the rarity of these events do not make it possible to infer a causal relationship between search organization and performance in the same way as it could be demonstrated by the experimental manipulation of search trajectories. Albeit such manipulation is not possible with spontaneous search tasks, it is possible in serial recall tasks specifically designed for this purpose [Bor et al., 2003; De Lillo, 2004; De Lillo, 2012; De Lillo & Lesk, 2010]. Thus in Experiment 2, we used our VR set-up in order to use for the first time a serial recall procedure in a three-dimensional navigational environment.

EXPERIMENT 2

Methods

The same apparatus and the same virtual environments developed for Experiment 1 were used in Experiment 2. The same 10 participants took part in both experiments. Experiment 2 took place 1 day after the completion of Experiment 1. The specific procedures used in Experiment 2 are described below.

Experiment 2 featured a presentation and a recall phase. In the presentation phase, one of the white spheres surmounting the poles turned red until the participant traveled through the environment and selected it by operating the wand. A second pole would then turn red until selected, and so on, until the nine poles had been visited. The recall phase then began. The starting position was reinstated and participants had to recall the sequence of the presentation phase by navigating throughout the foraging space and by selecting the poles in the same order. The spheres remained white at all times during this phase.

Each trial featured either the clusters or the matrix configuration of poles and the to-be-recalled sequences could either be structured or unstructured. Structured sequences in the clustered condition featured consecutive items within the same cluster until the cluster was exhaustively explored; unstructured sequences always had consecutive items in different clusters. Following Bor et al. [2003], structured sequences in the matrix condition had consecutive items within the same row, column, or diagonal, whereas non-structured sequences always violated this constraint. Participants received, in random order, six trials for each condition according to a 2 (configuration: clusters/matrix) \times 2 (structure: structured/unstructured) repeated measure design.

Results

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

Figure 2 shows the proportion of poles selected in the correct order in the four conditions of Experiment 2. A 2 (configuration) \times 2 (structure) ANOVA carried out on these values showed a higher level of recall in structured sequences, $F = 38.88$, $df = (1, 9)$, $P < 0.001$, $\eta_p^2 = 0.81$. Neither the effect of configuration nor the interaction structure by configuration proved significant.

A time analysis provided converging results. The mean response time (RT) for correctly selected poles in each condition is presented Figure 3.

The same ANOVA carried out on these values revealed faster RT for structured sequences, $F = 48.87$, $df = (1, 9)$, $P < 0.001$, $\eta_p^2 = 0.85$, but no effects of configuration or interactions.

Discussion

In Experiment 2 we implemented a serial recall task in a foraging environment. The results clarify that there is a dependency between organizational principles and spatial WM in humans under these testing conditions. Benefits of spatial structure in humans have been observed in ISSR tasks [Bor et al., 2003; De Lillo, 2004; De Lillo & Lesk, 2010] where the configuration of items is laid out in front of the observer and shown to play an important role in sequence encoding [Avons, 2007]. The results of this experiment indicate that the benefits of organization are also evident when people navigate through the set of locations in a large virtual foraging environment.

The size of the environment and the immersive VR set-up required the subjects to navigate through the environment in a way that determined a continuous change of perspective and view-point at any point of the exploration of the set or during recall. This made it possible to determine for the first time that effects of structure in spatial recall are not

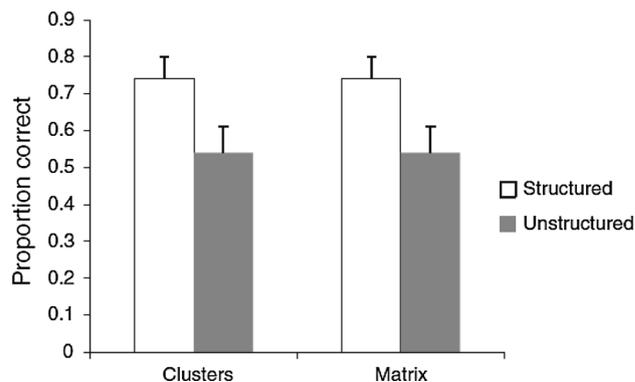


Fig. 2. Proportion of poles selected in the correct order in each condition of Experiment 2 and Error bars = 1 SE.

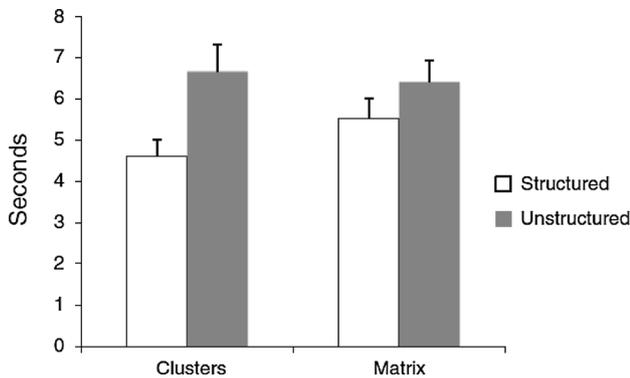


Fig. 3. Response time (RT) recorded in each condition of Experiment 2. Error bars = 1 SE.

confined to situations affording a bird's eye view of the configuration explored at any point during the task. However, in the task featured in Experiment 2 the length of the search path was not entirely independent from the degree of structure. In fact, in structured sequences the path length was often shorter than in non-structured sequences. There are several reasons for suspecting that path length may affect recall so that a shorter path length should be associated with better memory recall. The first is that this effect has been observed in small scale spatial serial recall tasks where participants use finger movements to tap on locations presented on a computer monitors in a given order [Parmentier et al., 2005]. Moreover, if we assume that shorter movements require typically less time to perform, a better recall of sequences characterized by a shorter path may be expected on the basis of working-memory models which assume a relationship between the time it takes to rehearse a sequence and its recall [see Smyth & Scholey, 1994, for a discussion of this point]. It was, therefore, important to assess if the length of the path used by the participants to explore the to-be-recalled locations in the present task affected accuracy and potentially confounded the results of Experiment 2. In order to assess this possibility, in Experiment 3 we dissociated path length and organization by manipulating the distance between the to-be-explored sites as well as the structure of the search path.

EXPERIMENT 3

Methods

A new set of participants took part in Experiment 3. They were eight male and eight female psychology undergraduate students from the University of Leicester ($N = 16$, M age = $21.13 \pm SD 2.88$ years, age range: 18–27) who received course credits for their participation. The general task was the same as that used in Experiment 2. However, the design of Experiment 3 featured the inter-pole distance as a

further variable, which was manipulated by changing the scale of the search environment while keeping the size of the poles and the objects in the environment constant. There were a long and a short inter-pole distance conditions. They will be referred to as long-path and short-path conditions hereafter, since they were used to affect the length of the path taken by the subjects in any particular trial. The inter-pole distance in the long-path condition was made three times as long as the short-path condition. In particular, the minimum possible distance between the poles was 2.1 m in the long-path condition and 0.7 m in the short-path condition. The starting distance from the centre of the array of poles in the long-path condition was 14.7 m and 4.9 m in the short-path condition. Figure 4 shows the two configurations and display sizes.

The inter-pole distances used in the short-path condition and in the long-path condition were calculated so that the long-path structured trials required walking a longer distance through the VR environment than in the short-path unstructured trials. Thus, for Experiment 3 a 2 (configuration: cluster/matrix) $\times 2$ (structure: structured/unstructured) $\times 2$ (inter-pole distance: short-path/long-path) repeated measure design was used.

As in Experiment 2, in each trial participants completed the presentation phase where they were required to navigate toward the pole which turned red and select it, until a sequence of visits to all nine poles was accomplished. Then a recall phase ensued, which required the participants to navigate throughout the environment to visit the poles in the same order. Participants received alternating trials of the short-path and long-path condition, with the starting condition randomized across participants. Apart from this constraint, the conditions were randomized across trials. Each participant received two trials per condition for a total of 16 trials. Participants were given a short break every two trials or when required and a 10 min break after eight trials. The definition of structure was the same as used in Experiment 2. The relative distance between poles in the cluster and the matrix condition was also the same as in Experiment 2.

Results

The proportion of items correctly recalled in the clustered condition is shown in Figure 5a, and in the matrix condition in Figure 5b.

A 2 (path length) $\times 2$ (configuration) $\times 2$ (structure) ANOVA carried out on the proportion of items correctly recalled showed a significant effect for structure, $F = 7.11$, $df = (1, 15)$, $P < 0.05$, $\eta_p^2 = 0.32$, supporting the results of Experiment 2. However, the effects for path length, $F = 3.55$, $df = (1, 15)$, $P = 0.08$, $\eta_p^2 = 0.19$, and configuration, $F = 0.08$, $df = (115)$, $P = 0.79$, $\eta_p^2 = 0.01$, were not significant. A paired-

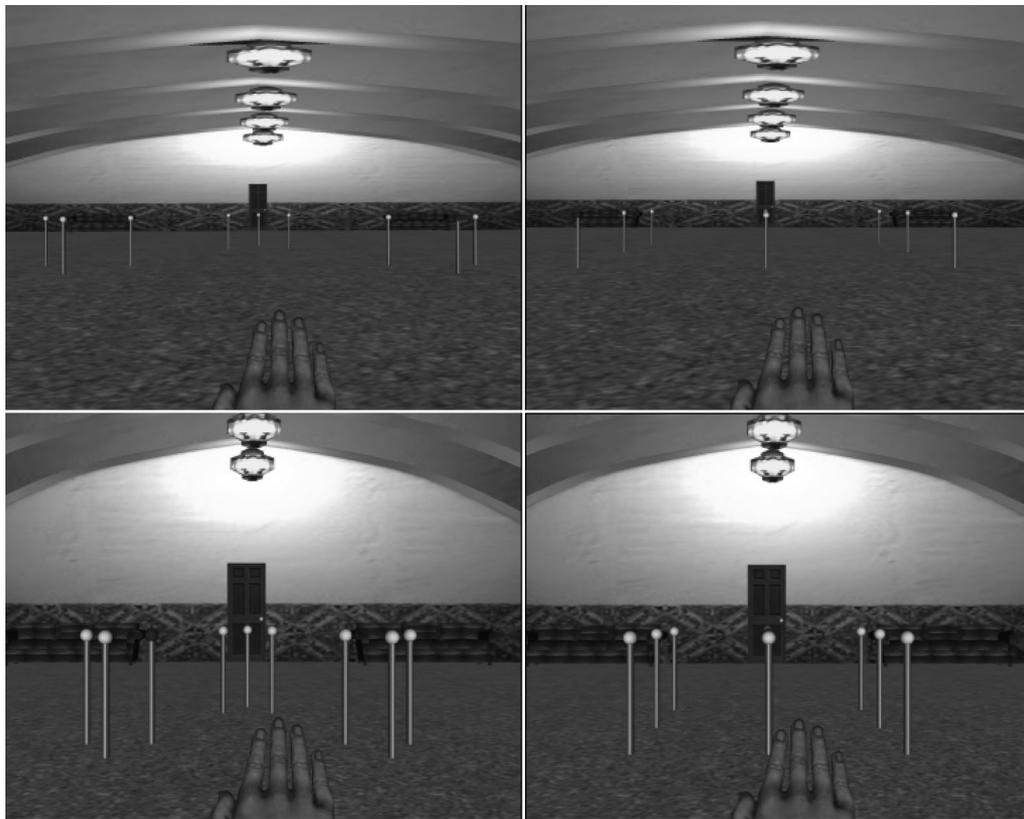


Fig. 4. Screen-shots of VR environments used in Experiment 3. Top row: large environments with long inter-pole and starting distance used for the long-path cluster (**left**) and matrix (**right**) conditions. Bottom row: small environments with short inter-pole and starting distance used for the short-path clustered (**left**) and matrix (**right**) conditions. See text for full explanations and measurements.

samples *t*-test was used to carry out the critical comparison between recall accuracy observed for short-path length unstructured trials and long-path structured trials, for both matrix and clusters. The *t*-tests showed that for the clustered array, structured sequences in the long-path condition ($M = 0.76 \pm SD 0.16$) were recalled with a higher level of accuracy than unstructured sequences with a short-path length ($M = 0.56 \pm SD 0.30$), $t = 4.00$, $df = 15$, $P < 0.05$. This demonstrates that structured sequences are easier to recall than unstructured sequences, even when their path-length is longer. In the matrix condition, the comparison between the recall accuracy for structured sequences with a long-path ($M = 0.64 \pm SD 0.32$) and unstructured sequences with a short path ($M = 0.59 \pm SD 0.29$) was not significant, $t = 0.67$, $df = 15$, $P = 0.51$.

As in Experiment 2, we carried out a time analysis that was based on correct responses only. One participant did not recall correctly any item in the clustered short-path unstructured condition. For this reason, there are 14 degrees of freedom for the error in the analyses reported below. For all poles selected in the correct order, the response times were obtained by averaging the means of the median response time observed in trials of each condition.

These values are shown in Figure 6a and b for the clustered and the matrix condition, respectively.

A 2 (path length) \times 2 (configuration) \times 2 (structure) ANOVA carried out on these values showed significant main effects of path length between the poles, $F = 127.73$, $df = (1, 14)$, $P < 0.001$, $\eta_p^2 = 0.90$, configuration of the poles, $F = 7.05$, $df = (1, 14)$, $P < 0.05$, $\eta_p^2 = 0.34$, and structure of the to-be-recalled sequence, $F = 35.86$, $df = (1, 14)$, $P < 0.001$, $\eta_p^2 = 0.72$. A significant interaction configuration by structure was also revealed, $F = 10.22$, $df = (1, 14)$, $P < 0.05$, $\eta_p^2 = 0.42$. A paired-samples *t*-test showed that for the long-path condition with the matrix configuration, there was no significant difference in time taken to recall sequences between unstructured ($M = 13.42 \pm SD 3.83$) and structured sequences ($M = 11.71 \pm SD 4.83$), $t = -1.79$, $df = 15$, $P = 0.09$. In the short-path condition however, unstructured sequences ($M = 6.79 \pm SD 2.02$) took significantly longer to recall than structured ($M = 5.45 \pm SD 1.86$), $t = -3.14$, $df = 15$, $P < 0.05$. For the long-path condition in the clustered configuration, the unstructured sequences ($M = 13.72 \pm SD 5.15$) took significantly longer to recall than structured sequences ($M = 7.23 \pm SD 2.00$), $t = -6.03$, $df = 15$, $P < 0.001$. The same pattern was observed in the short-path conditions for the

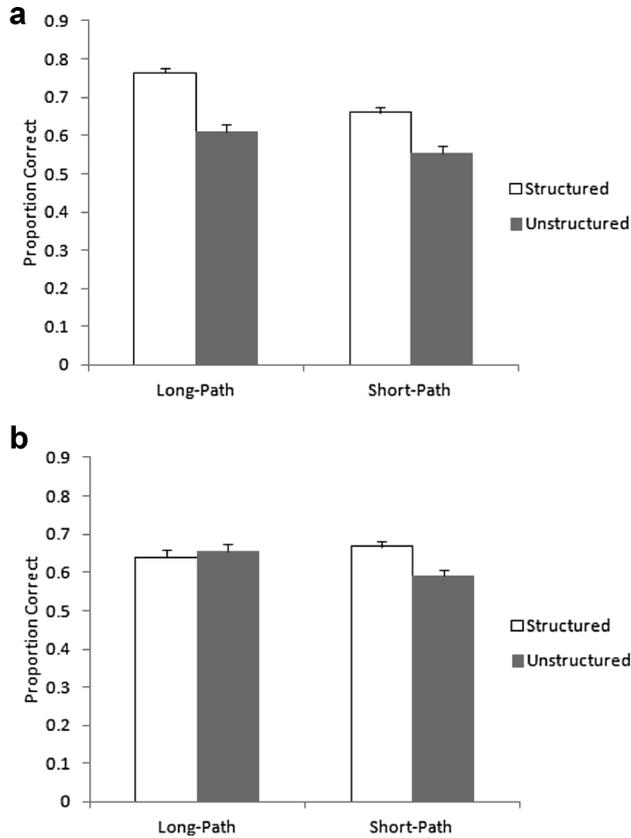


Fig. 5. Proportion of items correctly recalled in the clustered long and short-path conditions (a), and in the matrix long and short-path conditions (b) of Experiment 3. Error bars = 1 SE.

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

The comparison of long-path structured and short-path unstructured condition for both the matrix and clusters showed that the long-path structured sequences for the matrix took significantly longer to recall than then the short-path unstructured matrix, $t = 4.84$, $df = 15$, $P < 0.001$. There was no significant difference however in the clustered configuration between the long-path structured condition and the short-path unstructured condition, $t = -0.97$, $df = 14$, $P = 0.35$.

Discussion

The length of the movement path necessary to reproduce a sequence of responses in a small scale spatial array of locations, such as that used in variations of the Corsi test, has been shown to have an effect on spatial recall in humans [Parmentier et al., 2005]. Fagot and De Lillo [2011], observed a negative effect of path length in baboons tested in one of the first implementation of variation of the Corsi test in non-human primates. It was, therefore,

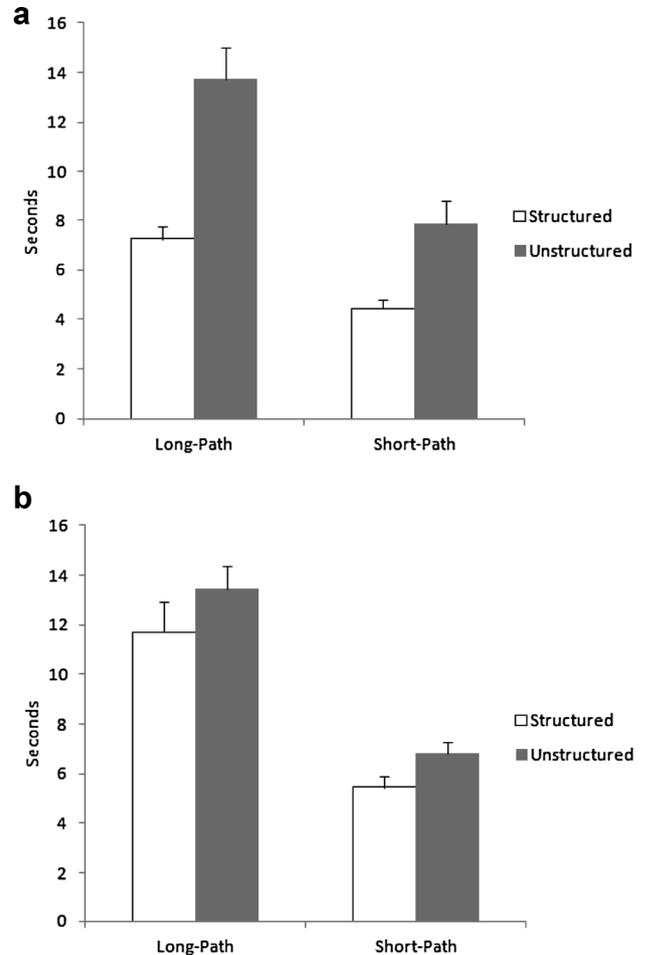


Fig. 6. Response time (RT) recorded in the clustered long and short-path conditions (a), and in the matrix long and short-path conditions (b) of Experiment 3. Error bars = 1 SE.

important to address the potential confounding effects of path length and use of spatial structure in the present study where they could have been present or even exacerbated in a task requiring virtual navigation in a larger search space. In Experiment 3 we tested the effect of path length with both the clustered and the matrix configuration. We compared the recall of structured and unstructured sequences characterized by a long or a short-path length. Importantly, we ensured that the structured sequences in the large arrays had a longer path length than the unstructured sequences in the small array. The results strongly suggest that path length cannot in itself explain the beneficial effects of path structure observed in Experiment 2. In fact, in the clustered configuration a more accurate recall was observed for structured sequences even when these had a longer path length than unstructured sequences. In the matrix condition, we observed a difference between these two critical conditions, which was in the same direction but did not reach statistical significance.

The time analysis confirmed that the pattern of results obtained for recall accuracy in the two critical conditions could not be explained on the basis of the time it took on average to select consecutive items. In fact, in the matrix array a longer median RT was observed in the long-structured condition compared to the short-unstructured condition. Yet these two conditions did not differ in recall accuracy. In the clustered array, similar RTs were observed in the long-structured condition and in the short-unstructured condition. Yet the recall accuracy in the former was higher than in the latter.

GENERAL DISCUSSION

In the present study, we carried out a series of three experiments with adult humans using immersive virtual reality foraging environments. The use of this technology allowed us to obtain information about human spatial WM that can be used in a comparative context. Moreover, immersive VR made it possible for the first time to implement a serial recall task within a foraging space. Serial recall enabled us to gain important additional information concerning the relationship between the use of organized paths throughout a search space and memory.

In the first instance, the results of the present study indicate that in a “patchy” foraging environment such as our clustered configuration humans spontaneously deploy a search strategy similar to that shown by capuchin monkeys [De Lillo et al., 1997], the only non-human primate species tested so far in such a task. This strategy is best defined as “clustering” and involves searching all the locations within a cluster before moving on to searching locations within another cluster. A similar tendency had been previously observed in 4-year old children tested in a real-life task analogous to that presented to the capuchin monkeys [De Lillo, 2012]. The fact that a similar strategy emerges in both species in the virtual reality task seem to indicate that overall the VR was capturing essential aspects of the real-life task.

In most tropical forest environments, food resources are distributed patchily in time and space. When given the opportunity to search food locations, macaques have been found to use the distribution of previously found food to anticipate further locations, an ability which would increase natural foraging success and efficiency [Hemmi & Menzel, 1995]. The ability to search efficiently in a patchy foraging space could be the expression of a specific adaptation shared by most primate species to recall and relocate patchy resources such as fruiting trees and this may have played a critical role in the evolution of primate cognitive abilities [Milton, 1993; Zuberbühler & Janmaat, 2010; see also Garber and Porter, this issue]. Elsewhere [De Lillo et al., 1998], we have

shown that capuchin monkeys are able to develop search strategies that enable them to exploit resources distributed in a variety of spatial arrangements and argued that they show a flexibility that seems to transcend the specific ability to benefit from a patchy distribution of food resources. Nevertheless, capuchin monkeys do not seem to be able to impose structure on a more diffuse foraging space such as a matrix of locations and do not fully exploit the linear constraints afforded by such a search space. The results of the present study show that humans are able to do so and as such seem to have a higher degree of flexibility in detecting and exploiting items distributed across a larger variety of search spaces. In fact, in contrast with capuchin monkeys, humans were extremely principled and proficient with an arrangement of locations configured as a square matrix. These results obtained in a free search task would be consistent with those showing a remarkable ability of humans to benefit from the constraints imposed by the linear organization of a matrix in serial recall tasks [Bor et al., 2003].

We have recently reported a difference between humans and baboons (*P. papio*) in the serial recall of items presented in locations defined by a virtual 5×5 square matrix on a computer monitor [Fagot & De Lillo, 2011]. Sequence structure and path length were manipulated in the same study. Humans proved to be particularly sensitive to structure as they recalled better sequences segmented according to the linear structure of the matrix but they were not sensitive to path length. In contrast, baboons’ serial recall was not affected by the structure of the sequences but improved for sequences with a shorter path length [Fagot & De Lillo, 2011]. In common with other traditional serial recall tasks, such as the Corsi test presented on computer monitors, the task used by Fagot and De Lillo [2011] offered a bird’s eye view of the spatial arrangement of the target locations and each of the locations to be selected was visible at all time during both the presentation of the sequence and its recall. As such, the ability to detect structural properties of the paths that had to be reproduced could rely on perceptual organization. In fact, it has been proposed that greater recall of sequences segregated by the linear organization of the set is due to forms of chunking based on perceptual grouping [Bor et al., 2003].

There is now a rich set of results obtained with capuchin monkeys, baboons, and humans that indicates important differences in the visual cognition of monkeys and humans in their readiness to perceive the global spatial organization of a collection of local elements [e.g. De Lillo et al., 2005, 2011; Deruelle & Fagot, 1997, 1998; Fagot & Deruelle, 1997; Spinozzi et al., 2003]. In some cases, differences have been identified in the readiness of humans and monkeys to use specific perceptual grouping cues [Fagot & Deruelle, 1997; Parron &

Fagot, 2007; Spinozzi et al., 2004, 2009]. Therefore, when ISSR tasks afford an aerial view of the array of locations differences between humans and monkeys could be reduced, in principle, to interspecies differences in perceptual grouping.

The current experiments provide important information concerning this point. They were carried out using serial recall in an immersive virtual reality environment that, as in a real-life foraging task in navigational space, afforded a continuous change of viewpoint during search or recall. Thus they clarify that humans are able to impose strategies that allow them to benefit from spatial structure in a task where the contribution of visual perceptual grouping processes is less obvious. If it was used in the present task, a bird's eye representation of the configuration of the search space would have needed to be actively constructed by the subjects on the basis of local viewpoints experienced through navigation. The exact nature of the memory code used to benefit from structure in humans cannot be evinced from the present results and it is a matter of further investigation.

Spatial structuring in a foraging space may be based on the formation of a mental image of the search space. It is possible that given the similarity of mental processes involved in visual perception and visual imagery postulated by some theories [e.g. Borst & Kosslyn, 2008; Kosslyn & Thompson, 2003], processes similar to perceptual grouping acting on mental images of the search space may still pertain to the explanation of effects of structure in our task. Monkeys seem to show similar patterns to humans in experiments on mental rotation which suggest that they may have the capability for mental imagery [Vauclair et al., 1993] and have the ability to modulate the perception of global spatial configurations of stimuli using top-down attentional processes [De Lillo et al., 2011]. As such they could in principle show effects similar to some of those observed here in humans. The comparative investigation of the extent to which humans and monkeys structure mental images in a similar way would be a topic of extreme interest. It could clarify whether differences in the ability to benefit from linear structures between humans and monkeys extend beyond visual organization to forms of memory coding of spatial information. This may have important implications for our understanding of the extent in which monkeys represent a good model of human non-verbal memory and cognition and of what could be uniquely human in this domain.

ACKNOWLEDGMENTS

We acknowledge financial support from Capital Investment Fund grant "Visual, spatial and motor cognition in virtual reality, computer generated, and other realistic environments" and Nuffield Founda-

tion URB/39517 "Spatial Working Memory for clustered sites in a Virtual Reality based search task"; and technical support from Kevin McCracken.

AUTHOR CONTRIBUTION

C.D.L. designed the experiments, analyzed the data, and wrote the article. M.K. ran Experiment 3, analyzed the data, and wrote the article. F.C.J. ran Experiments 1 and 2 and contributed to the data analysis as part of a Nuffield Foundation undergraduate research bursary.

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