



The Method of Loci in Virtual Reality: Explicit Binding of Objects to Spatial Contexts Enhances Subsequent Memory Recall

Nicco Reggente¹ · Joey K. Y. Essoe¹ · Hera Younji Baek¹ · Jesse Rissman^{1,2}

Received: 7 January 2019 / Accepted: 7 June 2019
© Springer Nature Switzerland AG 2019

Abstract

The method of loci (MoL) is a well-known mnemonic technique in which visuospatial spatial environments are used to scaffold the memorization of non-spatial information. We developed a novel virtual reality-based implementation of the MoL in which participants used three unique virtual environments to serve as their “memory palaces.” In each world, participants were presented with a sequence of 15 3D objects that appeared in front of their avatar for 20 s each. The experimental group ($N = 30$) was given the ability to click on each object to lock it in place, whereas the control group ($N = 30$) was not afforded this functionality. We found that despite matched engagement, exposure duration, and instructions emphasizing the efficacy of the mnemonic across groups, participants in the experimental group recalled 28% more objects. We also observed a strong relationship between spatial memory for objects and landmarks in the environment and verbal recall strength. These results provide evidence for spatially mediated processes underlying the effectiveness of the MoL and contribute to theoretical models of memory that emphasize spatial encoding as the primary currency of mnemonic function.

Keywords Memory enhancement · Method of loci · Virtual reality

Introduction

The method of loci (MoL), also commonly referred to as the memory palace technique, has long been appreciated as a highly effective mnemonic (Yates 1966), with most users reporting it to be helpful and engaging (Qureshi et al. 2014). Indeed, empirical studies spanning several decades have substantiated the centuries of anecdotal praise for the MoL’s effectiveness in bolstering mnemonic recall (Bower 1970; Briggs et al. 1970; Crovitz 1971; Dalgleish et al. 2013; McCabe 2015; Roediger 1980; Ross and Lawrence 1968), with one observing a sevenfold increase in ordered recall over a rote rehearsal method (Bower 1970). In light of such consistent efficacy, one might expect that

the MoL is a complicated, time-consuming mnemonic to implement, but in fact, it is rather straightforward. Instructions are typically given as some minor deviation of the following:

Close your eyes and imagine yourself walking through a familiar location (e.g., your childhood home). Imagine an object that you’d like to remember and place it somewhere (e.g., on the front doorknob). Walk, in your mind’s eye, to a new location and a place another to-be-remembered object in another location. When you want to remember the list of objects, simply retrace your path and observe the items in their placed locations.

Despite the fact that the MoL dates back to the ancient Greeks, there has been relatively little empirical research into the cognitive factors that underlie its efficacy. There are several possible ways in which the MoL could facilitate memory. Since the traditional implementation of the MoL takes place within one’s mental imagery, it stands to reason that this mnemonic technique may enhance memory in much the same way that pictures (Nelson et al. 1976) and text illustrations (Levin 1983) can boost memorability, putatively through dual coding of verbal and visual representations (Paivio and Csapo 1973). Given that MoL implementers traditionally choose a familiar location to place

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s41465-019-00141-8>) contains supplementary material, which is available to authorized users.

✉ Nicco Reggente
nreggente@gmail.com

¹ Department of Psychology, University of California, Los Angeles, Los Angeles, CA, USA

² Department of Psychiatry & Biobehavioral Sciences, University of California, Los Angeles, Los Angeles, CA, USA

objects, their memory increase could be due to their insertion of personal meaning into the information, a phenomenon known as the self-reference effect (Rogers et al. 1977). The chosen environments could also be embedded with personally relevant emotional contexts, which could heighten arousal and modulate memory consolidation (for review, see Hamann 2001). Furthermore, learning information from a first-person perspective could theoretically recruit autobiographical memory processes, which tend to engage different neural regions than those recruited during standard non-autobiographical memory tasks (Chen et al. 2017), and thus might serve to bolster recall. The importance of episodic perspective taking could also explain the efficacy of mnemonics that leverage narratives (Herrmann et al. 1973) and the observation that narratives presented with a consistent point of view result in better comprehension and memory (Black et al. 1979).

In light of traditional psychological investigations of learning, it is also plausible that the MoL mnemonic creates a “desirable difficulty” (Bjork 1994) that makes the learning process more effortful but ultimately serves to strengthen the associations that will later facilitate successful recall (Pyc and Rawson 2009). Another related factor could be an increase of time spent contemplating and elaborating on the to-be-remembered information, potentially harnessing “long-term working memory” to rapidly integrate incoming information with pre-existing knowledge or schemas (Ericsson and Kintsch 1995). Case-studies of world-class memory champions (Hu et al. 2009) seem to corroborate this claim (Hu and Ericsson 2012). However, a more-recent case study examined the verbal reports of an individual capable of memorizing and immediately recalling strings of up to 300 random digits and found that the champion’s trick was to create mental associations between physical locations and the to-be-remembered information (Ericsson et al. 2017). This latter result showcases the important role of spatial memory, which is thought to provide a “scaffolding” for binding and organizing knowledge about non-spatial information.

A framing of memory in terms of spatial processing is in line with evolutionary theories that posit that the creation of a mind was to engage in purposeful movement (Dennett 1993; Llinás 2001; Llinás and Ribary 2001; Wolpert and Ghahramani 2000) and the observation that the medial pallium, whose allocortex houses the hippocampal formation, continued to evolve alongside hominid navigation into novel terrain (Jacobs and Schenk 2003). As such, the hippocampus, whose involvement in episodic memory is well documented (Eichenbaum 2004; Rissman and Wagner 2012; Scoville and Milner 1957; Squire 1992; Squire and Zola 1996; Tulving and Markowitsch 1998; Vargha-Khadem et al. 1997), appears to have been originally utilized for specialized representations that provided an advantage in navigation (Murray et al. 2018) by generating a cognitive map that allowed for purposeful movement (e.g., acquire resources, avoid danger)—providing a memory for one’s own location and relation to environmental stimuli (O’Keefe and Nadel 1978).

Indeed, theoretical interpretations of research on spatial navigation and memory emphasize the primacy of space for the encoding of information (for review see Robin 2018). Much like the scene construction theory (Hassabis and Maguire 2007, 2009; Maguire and Mullally 2013; Mullally and Maguire 2014), this notion positions scenes as the primary currency of the hippocampus. In fact, it is difficult to envision any autobiographical memory without an accompanying spatiotemporal context (Moscovitch et al. 2016; Tulving 2002). Indeed, spatial information is often recalled earliest in the retrieval process (Hebscher et al. 2017). Adding important evidence to the notion that spatial processes are inherently and perhaps subconsciously recruited for the encoding of information, Constantinescu et al. (2016) demonstrated that the manipulation of abstract information (i.e., creating conceptual relationships) elicits the same activity patterns exhibited by grid cells, which are fundamental to purposeful navigation (Bush et al. 2015; Hafting et al. 2005). Relatedly, navigation through digital folders has been shown to recruit the same areas involved in real-world spatial navigation (Benn et al. 2015). While a full investigation into shared mechanisms used for the encoding of both spatial and episodic memory is beyond the scope of this article, it is important to note that, at minimum, spatial context has a dominant neural signature in the coding of events (Eichenbaum and Cohen 2014; Robin et al. 2018) and that spatial cues lead to quicker and more detailed memories (Hebscher et al. 2017; Horner et al. 2016; Merriman et al. 2016; Robin et al. 2016).

The important role of spatial information is also supported by functional neuroimaging work. One study found that participants who encoded information using the MoL later showed increased activation during recall in brain areas traditionally involved in the processing of spatial information, such as the parahippocampal gyrus and retrosplenial cortex (Kondo et al. 2005). Another study also found MoL use to elicit increased activity within the medial temporal lobe, as compared to a non-spatial mnemonic (Fellner et al. 2016). A study that compared brain activity during encoding between memory champions and control participants found that the champions (who typically report using spatial strategies) disproportionately recruited posterior hippocampal and medial parietal lobe regions known to support spatial memory (Maguire et al. 2003).

Disentangling the various factors that putatively support the efficacy of the MoL mnemonic is challenging given that participants typically rely on their mental imagery to implement the strategy. Not only are there notable individual differences in mental imagery ability (Cui et al. 2007; Kosslyn et al. 1984), but the size and uniqueness of the environment, the amount of time physically spent in the environment, and the emotional associations one has with the space all vary, in sometimes unquantifiable ways, across participants. As such, an operationalized investigation can benefit from an experimental approach that does not mandate the use of mental imagery for encoding. Indeed, previous investigations have strategized to counteract

individual differences by providing participants with standardized images or familiar nearby locations to use (Bower and Reitman 1972; Kliegl et al. 1990; McCabe 2015; Moè and De Beni 2005). While creative, such paradigms could theoretically eliminate some of the contributing variables of interest (e.g., volitional navigation).

An empirical investigation into the effectiveness of the MoL is plagued not only by the inherent inaccessibility of mental imagery, but also by the fact that people's use of effective mnemonic strategies is generally low (McCabe et al. 2013). Despite the well-intentioned endorsement of mnemonic improvement techniques being incorporated into curriculums (Balch 2005; Carney and Levin 1998; Shimamura 1984), such instructions may end in vain; undergraduates who are exposed to mnemonic strategies as part of their academic curriculum often do not implement those strategies into their study routines (Susser and McCabe 2013). This apparent mental barrier is quite noteworthy; even research subjects who receive explicit instructions to use the MoL have troubles complying (Legge et al. 2012). Perhaps also contributing to a lack of widespread adoption of the MoL, most studies report a need to have long training periods before the technique becomes effective (e.g., 4 to 6 h of training in the study by Brooks et al. 1993).

The present study was designed to both (a) test the hypothesis that the binding of information to a spatial scaffolding underlies the effectiveness of the MoL and (b) provide proof-of-concept for a user-friendly technology that mandates subject compliance in use of the MoL. The current investigation leverages virtual reality (VR), allowing participants to readily implement an MoL-based encoding strategy without the reliance on mental imagery. By providing a novel and common set of environments for participants, this study's VR-based paradigm mitigates the discussed concerns regarding individual differences in mental imagery, environmental size, complexity, and exposure time. Furthermore, VR serves as a particularly viable medium for increasing the ecological validity of memory experiments in general (Reggente et al. 2018) and allows for the control and capture of experimental details (e.g., exposure time and place of each seen object). A previous VR-based investigation by Legge et al. (2012), which exposed participants to virtual environments that were later used as "memory palaces" in a traditional mental-imagery-based implementation of the MoL, served as the foundation for utilizing virtual environments for both implementing the MoL and increasing participant compliance.

Methods

Participants

Sixty-seven participants were recruited for this study by way of posted flyers throughout the UCLA campus and listings on UCLA's online participant pool. Seven participants were

unable to finish the study in its entirety due to technical issues with the virtual reality software (e.g., objects did not appear or did not render completely). As such, a total of 60 participants, aged 18–27 ($M = 21$, $SD = 2.25$; 30 females), completed this study for either university course credit or cash payment.

Participants were required to be right-handed, have normal or corrected-to-normal vision and hearing, have a mastery of the English language, and report no diagnosed learning disabilities, substance dependencies, nor prescriptions for psychotropic medications. Additionally, to prevent unequal exposure to the experimental apparatus, applicants were not permitted to participate if they had more than 5 h of previous experience with the VR software used in this experiment (Second Life [<http://secondlife.com>] or its open-source virtual simulator OpenSimulator [<http://opensimulator.org>]). Eligibility screening was conducted prior to the participant's enrollment in the study using the Research Electronic Data Capture (REDCap) online survey system (Harris et al. 2009).

Participants were automatically assigned to one of two groups (MoL or WaL) based on gender and the order in which they were recruited for the study to ensure an even sampling of males and females within each group. The Institutional Review Board at UCLA approved all recruitment and testing procedures.

Materials

All tasks were presented on a 27" LG LED Monitor (1600 × 900 resolution; 60 Hz refresh rate) connected to a custom-built computer running a 64-bit Windows 7 Professional Operating System on an Intel® Core i7-3770K Central Processing Unit (CPU) at 3.50 GHz (8 CPUs) with 32GB of RAM and an AMD® Radeon Graphics Processor with 4GB of RAM. In pilot versions of this study, we explored the use of the Oculus Rift DK1 head-mounted display to create an even more immersive VR experience, but a high percentage of participants experienced nausea with this setup, whereas our single monitor setup was much more well-tolerated.

All virtual environments were created using OpenSimulator (<http://opensimulator.org>; Release 0.9.0.0)—an open-source virtual simulator of Second Life (<http://secondlife.com/>) and viewed using the Firestorm Viewer (The Phoenix Firestorm Project, Inc.; <http://www.firestormviewer.org/>; Release ×64 5.0.7.52912). Screen recordings of participant activity, for quality assurance purposes, were captured using FRAPS real-time video capture and benchmarking (Beepa Pty Ltd.; <https://www.fraps.com>; v3.5.99). A total of five distinct virtual environments (VEs) were custom-created for this study ("Toon World," "Ruin World," "Lagoon World," "Moon World," and "Avatar Island"; Fig. 1a). Despite being designed specifically to maximize distinctiveness, each VE that was used during encoding and encoding practice (all worlds except for Avatar Island)

was created with the exact same dimensions (a 64×64 grid of accessible space) and was populated with eight distinct landmarks at the cardinal perimeter points (i.e., North, Northeast, East, etc.; Fig. 1b).

Custom-coded software was created and “worn” by the participant’s avatar by way of two digital heads-up displays (HUDs). The first HUD rendered a count of collected and total tokens (Fig. 2a) on the participant’s screen. A total of 20 tokens were available for participants to collect in each VE: coins in Toon World, rings in Ruin World, and seashells in Lagoon World (Fig. 2a). All tokens were matched for color and size and scattered about each environment to ensure even exploration of the VEs. The release of these tokens was triggered by the experimenter via control desks located above the

environments (Fig. 2b). The control desk recorded the total time taken by the participant to collect all tokens in the environment.

The second HUD rendered a 3D object 1 m in front of the participant’s avatar (Fig. 3a), updating its position with each change in location and orientation until a participant clicked on the object, at which point the object would freeze in place unless clicked again. The object’s name appeared above each object in small white text. The experimenter used a separate “control desk” to control which objects would render in which order and for how long during each encoding. This control desk recorded the precise location of each item in the environment (x,y coordinates) with a temporal resolution of 1 s. A total pool of 60

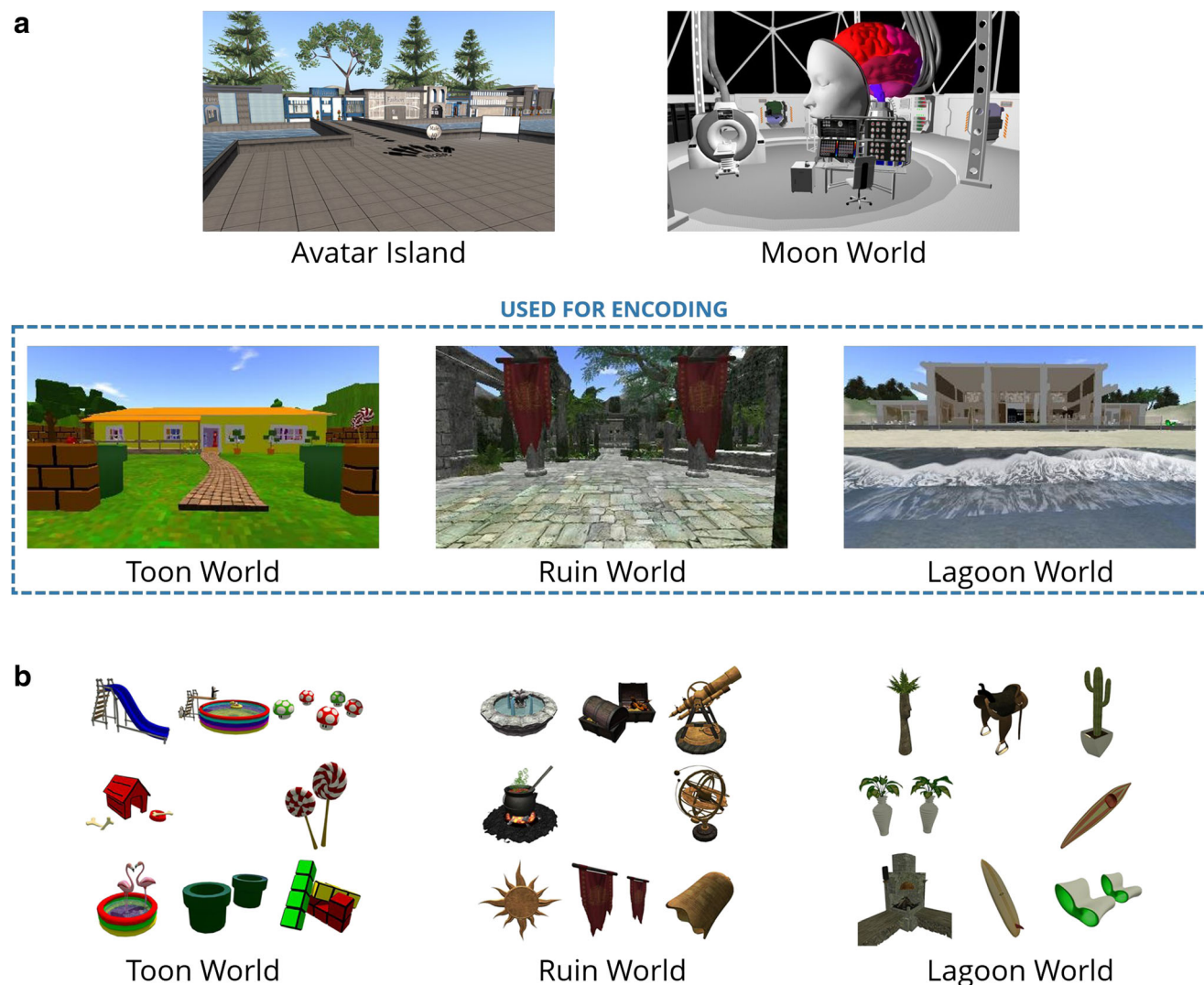


Fig. 1 Virtual environments and landmarks. **a** The five virtual environments (VEs) created for this study using OpenSim Software. Toon World, Ruin World, and Lagoon World were used for encoding. Viewpoints within encoding environments reveal the participant’s starting location in the southmost area of the world, facing north. Avatar Island was used to familiarize participants with navigation within our VEs and

Moon World was used to expose participants to the object-placement technology. All environments were situated within a 64×64 grid region border. **b** The 24 landmarks placed at the eight cardinal locations (N, S, W, E, NW, NE, SW, SE) along the perimeter of each of the three encoding VEs. The arrangement of each landmark in this figure reflects their placement within each environment

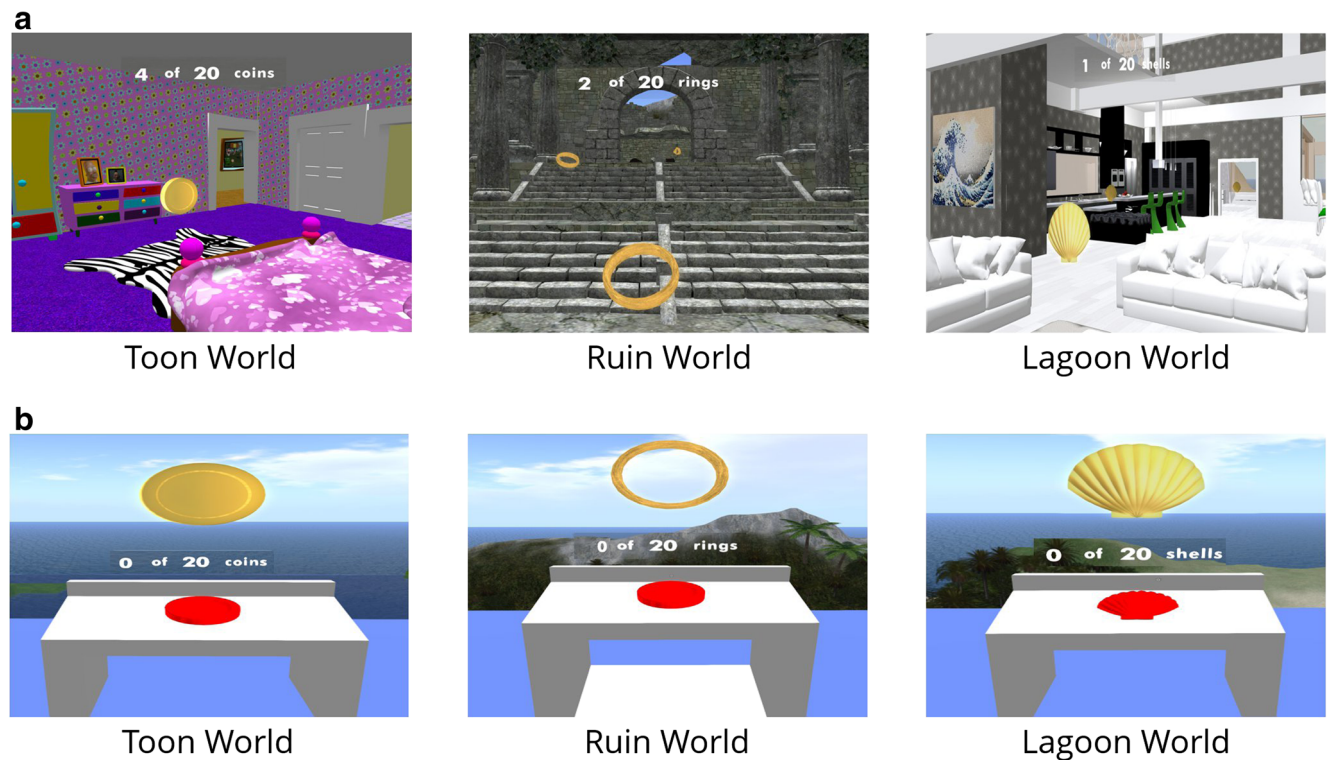


Fig. 2 Token collection task and software. **a** Prior to encoding the object lists, participants performed a token collection task to foster thorough exploration of each VE. A heads-up display (HUD) indicated a participant's progress as they collected each of the 20 "tokens" with each world (coins in Toon World, rings in Ruin World, and shells in

Lagoon World). **b** Experimenter control platform located above each environment, used for controlling the release of the tokens. Experimenters were able to use these control platforms to clear tokens, initiate the collection phase, and collect metrics of a participant's token collection behavior

3D open-source objects was gathered for this study from TurboSquid (<https://www.turbosquid.com>) and modified using Blender (<https://www.blender.org>). Objects were randomly sampled, without replacement, from this pool when creating the list of objects used for participant encoding. See [Supplemental Information Appendix 1](#) for a list of the objects used in this experiment.

Verbal recall tests were digitally recorded with participant permission and cued conversationally by experimenters. Spatial recall tests (Fig. 4) were conducted and analyzed using custom MATLAB (The Mathworks, Inc. 2012) code and Psychophysics Toolbox (Version 3; Brainard 1997), which allowed participants to view a bird's-eye view of the VEs and pinpoint their cursor to the cued location of landmarks, tokens, and objects they encountered. Finally, all statistical tests were conducted using custom R (R Core Team 2013; <http://www.R-Project.org/>) and MATLAB code.

Procedure

All participants were familiarized with our VR software by first visiting "Avatar Island" and practicing their use of a keyboard and mouse to navigate about and change their perspective in the VE. The experimenter allotted a maximum of 5 min

for the participant to showcase their ability to execute directed action with their avatar (e.g., move forward, turn around). Participants remained in first-person view during this orientation and throughout the duration of the experiment.

Following orientation, participants were teleported in a random order to the southern-most region of each VE used for encoding (Toon World, Lagoon World, Ruin World). Participants were instructed to navigate about each VE and "walk through" each token until all 20 were collected. Participants were given 5 min to collect the tokens and encouraged to further explore the environment with any remaining time, taking care to note any landmarks. After visiting each of the three VEs once, participants were teleported back, again in a random order, to the same starting locations. This time, participants were instructed to collect the tokens as quickly as possible and given a maximum of 3 min to do so.

After completing the second-round of token collection, participants were given group-specific encoding instructions. Participants in both groups were informed that a series of 15 objects would iteratively render in front of their avatar for 30 s each before disappearing and the subsequent object appearing. Prior to viewing each set of objects, participants were told that the objects they were about to see belonged to one of three fictional individuals (Otto, Pike, or Viola) and that they would

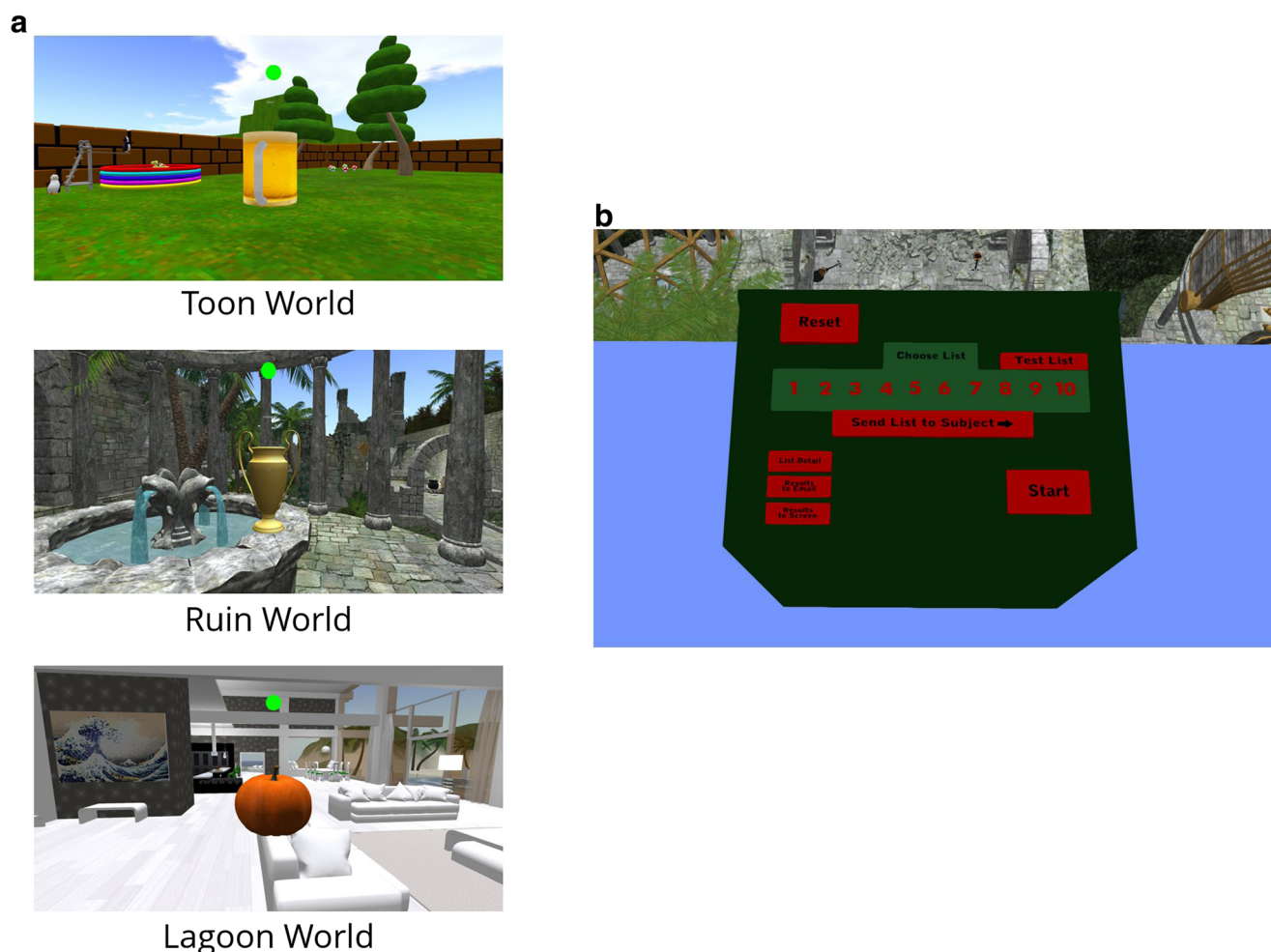


Fig. 3 Object encoding task and software. **a** Objects continually rendered in front of participants as they navigated about each encoding environment. A heads-up display (HUD) rendered the objects and provided a light (green shown here) indicating whether participant was currently in the encoding phase. Each object was visible for a period of 20 s before disappearing and a new object appearing in its place. Participants were able to view the object from all angles of its pitch and yaw axes by rotating about the object. Participants assigned to the MoL

group were given the additional instructions to click on each object to “freeze” it in a location of their choosing. Shown here is a beer in Toon World, a trophy in Ruin World, and a pumpkin in Lagoon World. **b** Experimenter object-control platform, located on a platform floating above each environment. Experimenters were able to use these control platforms to load in participant/environment-specific lists of objects, send objects to the participant’s HUD, and collect metrics of each object’s location within the environment at a temporal resolution of 1 s

later be asked to recall the list of items belonging to that individual, in the order in which they were originally presented. Which objects were on each list, which fictional individual was associated with that list, and the environment in which the list was encoded were randomized for each participant. All participants were encouraged to walk about the environment while viewing the objects; the objects would remain in front of the avatar regardless of movement and view.

Participants assigned to the “Walk and Learn” (WaL) group were informed that they would be experiencing the benefits of “active learning” as they navigated through each virtual world and attempted to memorize each set of 15 objects. Although this is not the traditional meaning of the phrase “active learning,” it was presented to participants as a well-documented memory enhancement procedure that they could take advantage of while learning in VR. This information was relayed to participants in

order to counteract any potential effects of anticipated task demands (Rummel and Meiser 2013) or performance (Bandura 1993; Martell and Willis 1993) that would otherwise be specific to the MoL group. In contrast, participants in the MoL group were briefed on the classic implementation and effectiveness of the MoL technique and told they would be employing the MoL strategy using a suite of VR tools. Critically, MoL participants were given the additional instruction to click on each object to “freeze” it in a location of their choosing, allowing the participant the freedom to navigate away from the stationary object until its disappearance. For a complete transcript of each group’s instructions, see [Supplemental Information Appendix 2](#).

After receiving instructions, but prior to encoding the lists of objects, participants were teleported to Moon World where they practiced the viewing and placement (for MoL participants) of three geometrical objects (sphere, cube, pyramid).

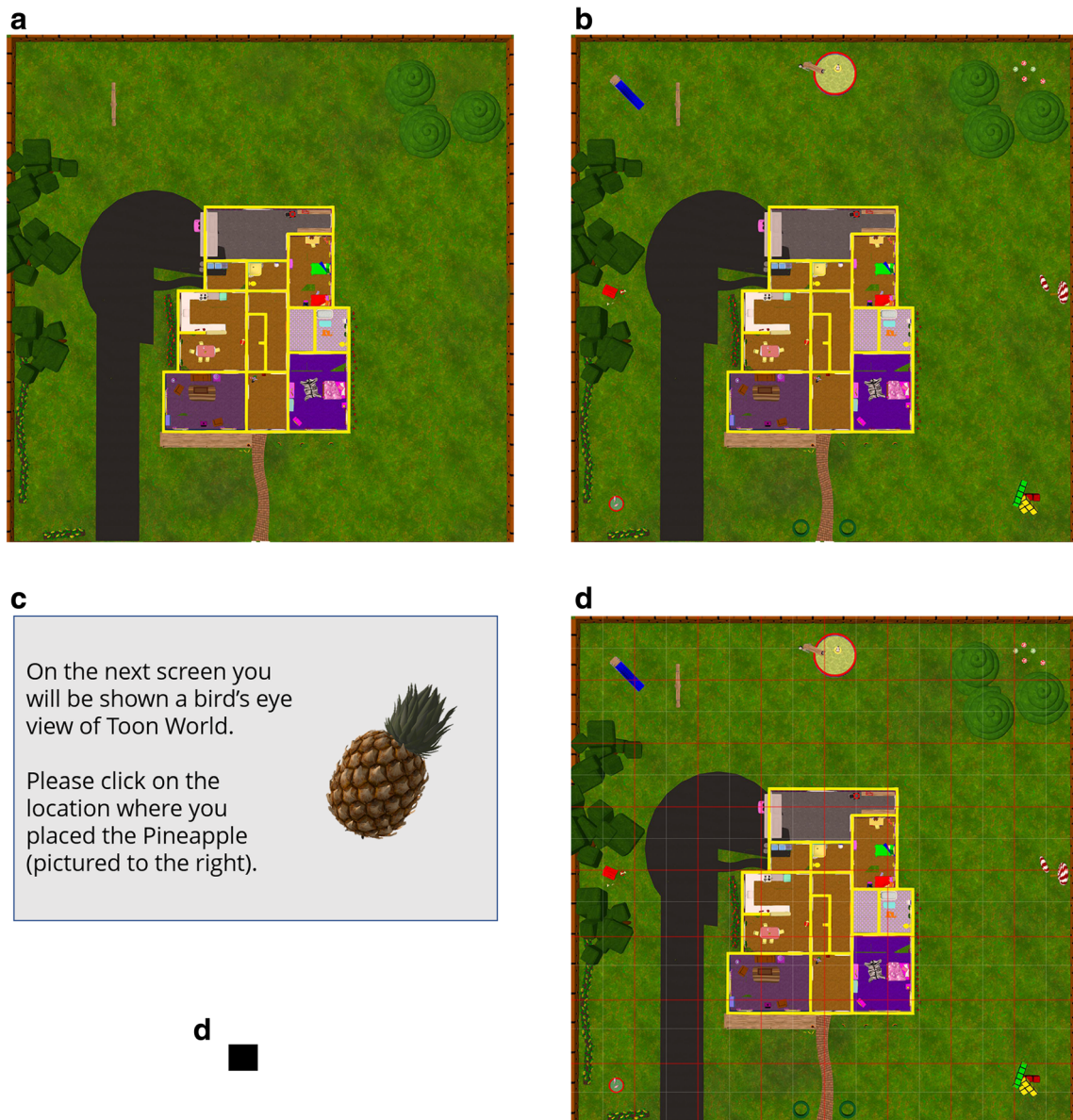


Fig. 4 Object/landmark/token-placement task. Following the free recall phase of the experiment, participants were shown an allocentric “bird’s eye” view of each environment (Toon World shown here). In one version (a), used for the landmark-placement task, the view was stripped of its 8 peripheral landmarks while in the other version (b), used for the object-placement and token-placement tasks, the view contained the landmarks. c The instruction screen immediately preceding each placement trial. Participants were provided with a 2-D image of an object they encoded

and instructions to click on the map location where they placed (MoL group) or last saw (WaL group) the object. d The mouse cursor (displayed as a black rectangle) that participants used to select the location of the cued object/landmark/token. e A grid overlay delineating the 4096 (64×64) cells available for participant selection via their cursor. This grid was not visible to participants, but could be inferred given the cursor’s inability to be placed outside of each cell—the cursor would “snap” to fit into the nearest, overlapping cell.

Subsequently, participants encoded a total of three lists of 15 objects across the three encoding environments. Following this encoding period, participants were given a short 2-min break. Afterwards, participants were cued to recall the items belonging to each of the fictional individuals in order to prevent an experimenter-driven direct association between objects and the environment during recall. They were given a maximum of 2 min and encouraged to recite as many objects as they could in the case that they could no longer retain a

temporal order to their recall. Following each recall attempt, the participant was asked to recall the same list of items, but in the reverse order—starting with the last item on the fictional-individual’s list and ending with the first. As with forward recall, participants were allotted 2 min for reverse-recall and were informed they could recall items out of order if need be. Recall list order was randomized across participants.

As a final test, participants performed a spatial memory task (Fig. 4) where they indicated the last seen location (WaL group)

or last placed location (MoL group) of each object. Specifically, participants used the computer mouse to direct a rectangular cursor and indicate the location of a cued object on a bird's-eye view of the encoding environment—a perspective they had never encountered during the encoding period. Each object and its name was shown on a prompt screen before showing the full-screen map. After providing responses for each object encoded within a given environment, participants were asked to indicate the location of each landmark and then each token before moving on to the next environment. During the landmark portion of this spatial memory task (“landmark-placement task”), the map was stripped of its landmarks. During the token portion (“token-placement task”), participants were asked to indicate the location of each of the 20 tokens and show the locations of each of their preceding choices. The presentation order of objects, landmarks, and environments for spatial tasks was randomized across participants. See Fig. 5 for a visualization of the experimental procedure.

Behavioral Scoring

Participants' verbal recall was transcribed and scored by two separate experimenters and discrepancies were resolved by a third. All recall metrics are reported as the total words recalled across the three lists (45 total words). Recall strength was assessed using three metrics: number of words recalled (Recall_{TOTAL} or Reverse-Recall_{TOTAL}) and number of words recalled in the correct order (Recall_{CLUST} or Reverse-Recall_{CLUST}). Recall_{TOTAL} was defined by the total number of words recalled before the time limit by a participant—only counting words that actually belonged to the cued fictional individual. Clustering (Recall_{CLUST}) was calculated using a serial clustering metric, adjusted for chance, developed by

(Stricker et al. 2002) and given by:

$$\text{Clustering} = X - (r - 1) / N$$

where X is the total number of observed pairs of adjacent words in the recalled list that were also beside each other in the original presentation list, r is the total number of correct words recalled in the trial, and N is the total number of words presented in a list ($N = 15$ in all calculations). Using this metric, the amount of serial clustering expected by chance (the $(r-1)/N$ portion of the equation) during verbal recall is a fraction less than one, suggesting that serial clustering is not highly expected by chance.

Behavioral metrics from the spatial memory task were calculated as the average Euclidean distance between the coordinate vectors (x, y) for an object's actual placed location (MoL group) or last-seen location (WaL group) in the environment and that indicated by the participant. A metric denoting the average proximity of objects to landmarks within an environment was calculated as the Euclidean distance between an object and its nearest landmark. Finally, a “base metric” for each participant's spatial memory was calculated as the difference in time taken to collect all the tokens throughout each environment from the first and second attempts. Given that token collection was conducted before groups received encoding instructions, this measure should reflect an individual's baseline spatial memory.

Presence

A six-question survey, developed by Slater and colleagues over the course of several investigations (Supplemental Information Appendix 3; Slater et al. 1998, 1994, 1995a, b), was used as a measure of presence—the subjective sense of experiencing a VE as a place that one is actually inhabiting,

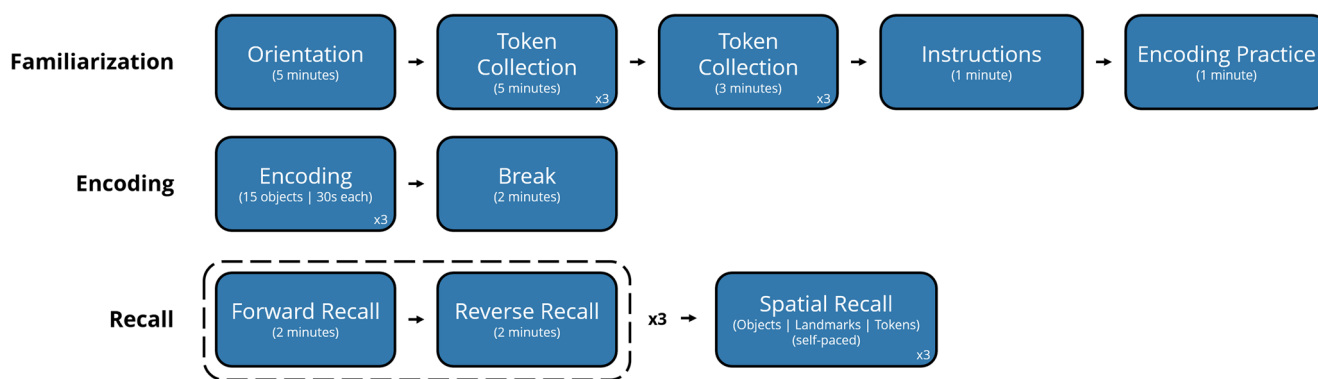


Fig. 5 Experimental paradigm. All participants underwent a familiarization phase that first included a general orientation in Avatar Island, followed by 5 min of token collection in each of the three encoding environments and then a 3-min period of token collection that emphasized collection speed. If participants completed token collection before the time limit was up, they were encouraged to explore the environments until time expired. Afterwards, participants were read group-specific instructions and teleported to Moon World to practice encoding (viewing and walking for WaL group; viewing, walking, and placement

for MoL group). All participants then encoded a list of 15 objects in each of the three environments. After the third encoding session, participants were given a short 2-min break. Following this break, participants were cued to verbally recall each list of items in their forward encoding order and, immediately thereafter, in their reverse encoding order. After forward and reverse-recall sessions for each of the three lists, participants were submitted to spatial recall tests for object, landmarks, and tokens encountered in each environment. For any phase of the experiment that required a cycling through the three VEs, visitation/testing order was randomized

rather than something that one is simply watching on a screen. A metric was calculated for each participant as the number of responses that were rated to be ≥ 6 and is referred to hereafter as Presence_{SLATER}. A separate ten-item, five-point scale questionnaire that was derived from multiple sources and was intended to quantify a participant's level of presence was also used (Supplemental Information Appendix 4; Fox et al. 2009). A metric was calculated for each participant as the average score across all ten items and is referred to as Presence_{FOX}. Both measures of presence were collected during a post-experimental questionnaire using REDCap (Harris et al. 2009). Finally, to assess the potential impact of environment on presence, participants were asked to provide a ten-point scaling in response to the following question form for each world: "To what degree did you feel you were 'in' (Toon/Lagoon/Ruin) World as you moved around?"

Statistical Analyses

Analyses were conducted using a one-way analysis of variance (ANOVA) whenever comparing means of two or more independent groups of data (e.g., MoL vs. WaL recall metrics) and the F -statistic is reported as well as its associated p value. Results are reported as "effect of (independent variable) on (dependent variable)". Significant effects ($p < 0.05$) were followed-up with independent samples t tests (equal variance not assumed). Cohen's effect sizes (d) are reported where applicable (i.e., group comparisons) for significant results. The strength and direction of associations between two continuous variables were conducted by computing Pearson's linear correlation coefficient (r) and p values are reported from a t test comparing that coefficient to the null hypothesis of no relationship (i.e., $r = 0$). Resulting p values for all correlations were submitted to a family-wise multiple comparisons corrections using the Benjamini-Hochberg method (Benjamini and Hochberg 1995); correlations including the Recall_{TOTAL} and Recall_{CLUST} metrics were treated as the two families of tests and corrected p values are reported for correlations containing these metrics. Direct comparisons between two correlations were conducted in the presence of a significant correlation within any group to determine if (a) the groups differed as a function of their relationship to the metric of interest or (b) one group was driving the effect observed across all participants. Significance of correlation comparisons was assessed using a two-tailed test for the difference between either two independent correlation coefficients (e.g., MoL free recall and MoL object-placement memory vs. WaL free recall and WaL object-placement memory) (Cohen and Cohen 2003) or two dependent correlations with one variable in common (e.g., MoL free recall and MoL object-placement memory vs. MoL free recall and MoL coin collection time difference) (Steiger 1980) using an online utility ([http://quantpsy.org/corrtest/](http://quantpsy.org/corrttest/); Lee and Preacher 2013; Preacher 2002). For

analyses where multiple metrics were collected for each group (e.g., landmark-object proximity across worlds), a multivariate analysis of variance (MANOVA) was conducted and the F -statistic and Wilk's Λ are reported.

Finally, a stepwise linear regression was implemented to examine the impacts of additional variables on a linear model of group on recall metrics. Independent variables of interest were those that were either previously revealed to show a group difference (e.g., spatial memory) or were of general interest due to supporting literature (e.g., gender). An analysis of deviance was conducted on the nested models to determine the most parsimonious model; F -statistics reflecting the difference between the models and the associated p values are reported; beta-coefficients were analyzed with a t test.

Results

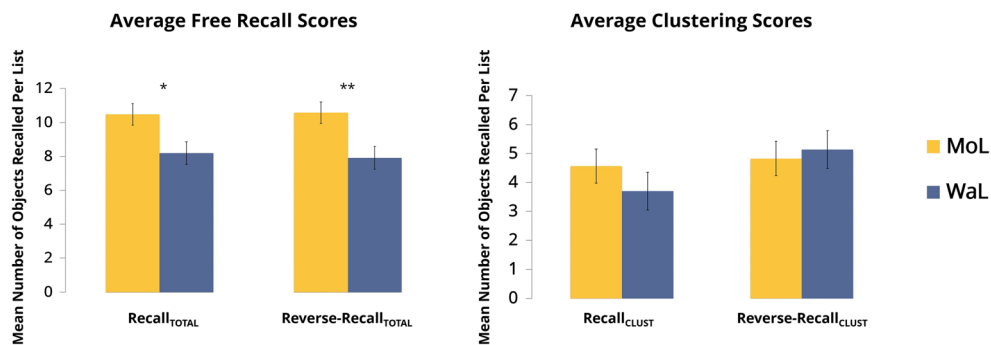
Verbal Recall

Participants assigned to the MoL group had an average Recall_{TOTAL} score of 10.49 words compared to 8.20 words for participants in the WaL group. The effect of group on Recall_{TOTAL} was significant [$F_{(1,58)} = 6.20, p = 0.02, d = 0.64$]. This group difference was even more pronounced during reverse recall. The MoL group had an average Reverse-Recall_{TOTAL} score of 10.59 words compared to 7.92 words by the WaL group and the effect of group on Reverse-Recall_{TOTAL} was significant [$F_{(1,58)} = 7.35, p = 0.009, d = 0.70$]. There was no effect of encoding environment on Recall_{TOTAL} within the MoL group [$F_{(2,89)} = 0.13, p = 0.88$] or WaL group [$F_{(2,89)} = 0.01, p = 0.99$]. The effect of encoding environment on Reverse-Recall_{TOTAL} within the MoL [$F_{(2,89)} = 0.02, p = 0.98$] and WaL [$F_{(2,89)} = 0.04, p = 0.96$] groups also remained null. There was no effect of group on Recall_{CLUST} [$F_{(1,58)} = 1.04, p = 0.31$] even though MoL participants had a numerically higher mean Recall_{CLUST} score of 4.57 compared to 3.70 for the WaL group. There was also no effect of group on Reverse-Recall_{CLUST} (MoL = 4.83; WaL = 5.14) [$F_{(1,58)} = 1.04, p = 0.31$] (Fig. 6). Recall_{TOTAL} and Reverse-Recall_{TOTAL} scores were highly correlated within both the MoL ($r = 0.92, p < 0.001$) and WaL ($r = 0.96, p < 0.001$) groups. Similarly, high correlations were observed for the Recall_{CLUST} and Reverse-Recall_{CLUST} in both the MoL ($r = 0.92, p < 0.001$) and WaL ($r = 0.84, p < 0.001$) groups.

Spatial Memory

Participants took significantly less time to collect tokens on their second attempt in each world (Ruin_{RUN1} = 121.0 s, Ruin_{RUN2} = 88.30 s, $t_{(118)} = -8.44, p < 0.001$; Toon_{RUN1} = 188.35 s, Toon_{RUN2} = 133.17 s, $t_{(118)} = -6.54, p < 0.001$; Lagoon_{RUN1} = 231.08 s, Lagoon_{RUN2} = 154.01 s, $t_{(118)} = -$

Fig. 6 Free recall performance. Average number of objects recalled per list ($Recall_{TOTAL}$) and average sequential clustering score ($Recall_{CLUST}$) as a function of group (MoL vs. WaL). * $p < 0.05$, ** $p < 0.01$



6.924, $p < 0.001$) (Fig. 7c). There was no effect of group on token-collection improvement (Run 1 time – Run 2 time) in either Ruin World (MoL = 31.69 s; WaL = 33.70 s) [$F_{(1,59)} = 0.09$, $p = 0.77$], Toon World (MoL = 66.77 s; WaL = 43.6 s) [$F_{(1,59)} = 2.26$, $p = 0.14$], or Lagoon World (MoL = 81.40 s; WaL = 72.73 s) [$F_{(1,59)} = 0.18$, $p = 0.67$] (Fig. 7a). Collapsing across environments, the effect of group on token-collection

improvement remained null [$F_{(1,58)} = 2.24$, $p = 0.14$ —suggesting that the groups did not differ in their baseline spatial memory prior to encoding (Fig. 7b).

When tested on their ability to remember the specific spatial locations where they had placed each object (MoL group) or where each object was last seen (WaL group), MoL participants had a significantly lower average Euclidean distance (in

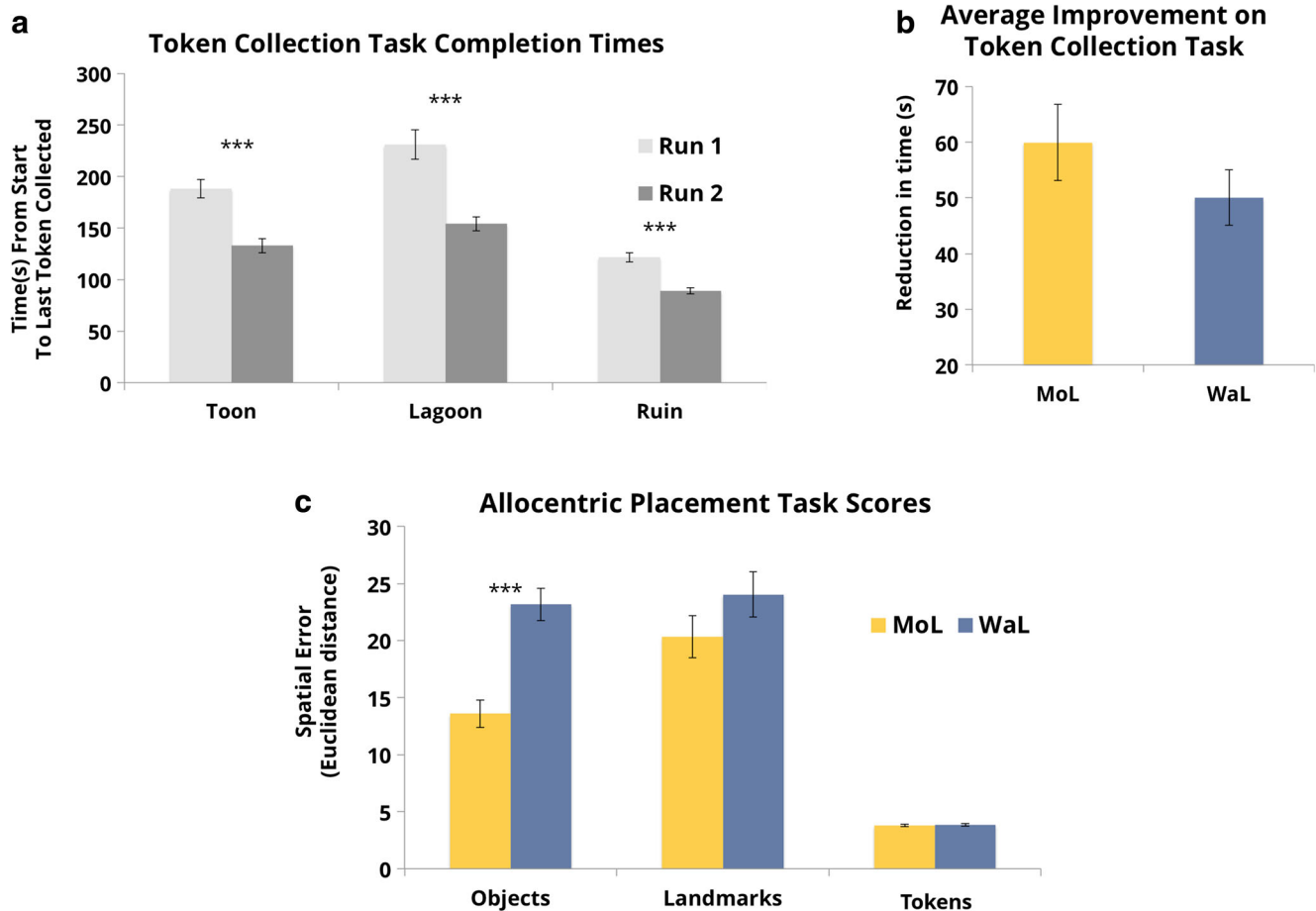


Fig. 7 Spatial memory performance. **a** Participant performance on the object-placement, landmark-placement, and token-placement tasks, as a function of group. Error was defined as the average Euclidean distance between where a participant indicated they had placed (MoL) or last seen (WaL) a cued object vs. the actual location of that object in the corresponding VE. The same analysis was used to probe participant memory for an environment’s static features: landmarks and coins.

Lower average Euclidean distance (error) indicates superior spatial memory. **b** Average improvement on the token collection from Run 1 to Run 2, as a function of group. Reduction in time is reported in seconds as (Run 1 time from start to last-token collected) – (Run 2 time from start to last-token collected). **c** Time to completion, defined as time from start to last-token collected, as a function of Run, collapsed across groups. *** $p < 0.001$

arbitrary units, based on the 64×64 virtual grid) between the remembered and actual locations of each object (i.e., better spatial memory) compared to WaL participants (MoL = 13.60; WaL = 23.18) [$F_{(1,58)} = 26.15, p < 0.001, d = 1.32$]. There was no effect of group difference on spatial memory for landmarks (MoL = 20.32; WaL = 24.05) [$F_{(1,58)} = 1.88, p = 0.18$] or coins (MoL = 3.78; WaL = 3.82) [$F_{(1,58)} = 0.06, p = 0.80$] (Fig. 7c).

Adding a participant's average object-placement error score to a linear model of group on $\text{Recall}_{\text{TOTAL}}$ significantly increased the model's explanatory power [$F_{(2,56)} = 9.826, p < 0.001$]. Adding a participant's object-placement error to a linear model of group on $\text{Recall}_{\text{CLUST}}$ [$F_{(2,56)} = 7.59, p < 0.001$] also increased the model's explanatory power.

Relationship Between Verbal Recall Performance and Spatial Memory

Participants assigned to the MoL group showed a strong relationship between $\text{Recall}_{\text{TOTAL}}$ and error on the object-placement task ($r = -0.57, p = 0.004$). Participants assigned to the WaL group also showed a significant negative correlation between $\text{Recall}_{\text{TOTAL}}$ and error on the object-placement task ($r = -0.45, p = 0.024$), but this relationship did not differ from the correlation observed when using MoL participants ($z = -0.61, p = 0.54$) (Fig. 8a). The relationship between $\text{Recall}_{\text{TOTAL}}$ and spatial error on the landmark-placement task was significant in both MoL ($r = -0.66, p = 0.004$) and WaL ($r = -0.45, p = 0.024$) participants; the difference in correlations between MoL and WaL participants was not significant ($z = -1.09, p = 0.275$) (Fig. 8b). Performance on the coin-placement task was significantly correlated with $\text{Recall}_{\text{TOTAL}}$ in the MoL group ($r = -0.437, p = 0.04$), but not the WaL group ($r = -0.35, p = 0.08$). However, the difference in these correlations was not significant ($z = -0.37, p = 0.71$).

MoL group participants' performance on the object-placement task correlated strongly with their $\text{Recall}_{\text{CLUST}}$ ($r = -0.62, p < 0.001$). Within the WaL group, there was no relationship between the object-placement task and $\text{Recall}_{\text{CLUST}}$ ($r = -0.34, p = 0.14$). Despite this difference, the WaL group's relationship between $\text{Recall}_{\text{CLUST}}$ and object-placement scores did not differ significantly from the MoL group ($z = -1.55, p = 0.13$). Performance on the landmark-placement task was not related to $\text{Recall}_{\text{CLUST}}$ in the MoL group ($r = -0.403, p = 0.14$) nor the WaL group ($r = -0.37, p = 0.14$). Performance on the coin-placement task did not show a significant relationship with $\text{Recall}_{\text{CLUST}}$ in neither the MoL ($r = -0.08, p = 0.82$) nor WaL ($r = -0.26, p = 0.28$) groups. There was no significant correlation between MoL participants' baseline spatial memory and $\text{Recall}_{\text{TOTAL}}$ ($r = 0.11, p = 0.63$) nor $\text{Recall}_{\text{CLUST}}$ ($r = 0.01, p = 0.96$). The same pattern was observed in WaL participants: $\text{Recall}_{\text{TOTAL}}$ ($r = 0.183, p = 0.4$), $\text{Recall}_{\text{CLUST}}$ ($r = 0.232, p = 0.31$). See Table 1.

Object-Landmark Proximity

In an attempt to determine if major environmental features, like the 8 landmark objects placed around the periphery of each virtual world, provided participants with a special opportunity to create memorable object-landmark associations, we examined whether participants' placement of to-be-remembered objects near landmarks varied as a function of group. A MANOVA revealed no significant effect of group on environment-specific proximity of objects to landmarks [$F_{(2,57)} = 0.84, p = 0.44$; Wilk's $\Lambda = 0.97$] (Fig. 9). Collapsing across environments revealed no effect of group on proximity of objects to landmarks [$F_{(1,58)} < 0.01, p = 0.99$]. When examining the effects within each group, there was a significant effect of encoding environment on the proximity with which objects were placed to landmarks in the MoL group [$F_{(2,89)} = 44.91, p < 0.001$]. This observation was driven by a marked average decrease in an object's Euclidean distance to the nearest landmark in Ruin (7.923) compared to Toon (15.454; $t_{(58)} = 7.53, p < 0.001$) and Lagoon (12.389; $t_{(58)} = 4.467, p < 0.001$); the difference between Toon and Lagoon was also significant ($t_{(58)} = 3.065, p < 0.001$). There was also a significant effect of encoding environment on the proximity with which objects were placed to landmarks in the WaL group [$F_{(2,89)} = 66.42, p < 0.001$]. Again, the effect was due to a closer proximity of objects to landmarks in Ruin (8.52) compared to Toon (15.188; $t_{(58)} = 6.668, p < 0.001$) and Lagoon (12.085; $t_{(58)} = 3.566, p < 0.001$); the difference between Toon and Lagoon was also significant ($t_{(58)} = 3.103, p < 0.001$).

MoL participants' $\text{Recall}_{\text{TOTAL}}$ showed no correlation with object-landmark proximity ($r = -0.01, p = 0.96$); neither did WaL participants ($r = 0.36, p = 0.08$). No correlation with object-landmark proximity was seen in $\text{Recall}_{\text{CLUST}}$ (MoL: $r = -0.06, p = 0.82$; WaL: $r = 0.34, p = 0.14$). Given the high correlation between forward and reverse recall, comparisons of Reverse- $\text{Recall}_{\text{TOTAL}}$ and Reverse- $\text{Recall}_{\text{CLUST}}$ to spatial memory metrics revealed largely similar findings (Supplementary Materials: Additional Results).

Effect of Gender

Adding a participant's gender to a linear model of group and object-placement spatial memory on $\text{Recall}_{\text{TOTAL}}$ significantly increased the model's explanatory power [$F_{(4,52)} = 4.29, p < 0.01$]. Upon further examination, the interaction term representing object-placement spatial memory and gender was the only significant coefficient [$t_{(58)} = -2.49, p = 0.02$]. The correlation of $\text{Recall}_{\text{TOTAL}}$ with object-placement spatial memory in males ($r = -0.26, p = 0.075$) was much lower than that observed in females ($r = -0.72, p < 0.001$)—a difference that achieved significance ($z = 1.99, p < 0.05$) and suggests that females were driving the interaction. Adding a participant's gender to a linear model of group and object-placement spatial memory on Reverse- $\text{Recall}_{\text{TOTAL}}$ also significantly increased the model's

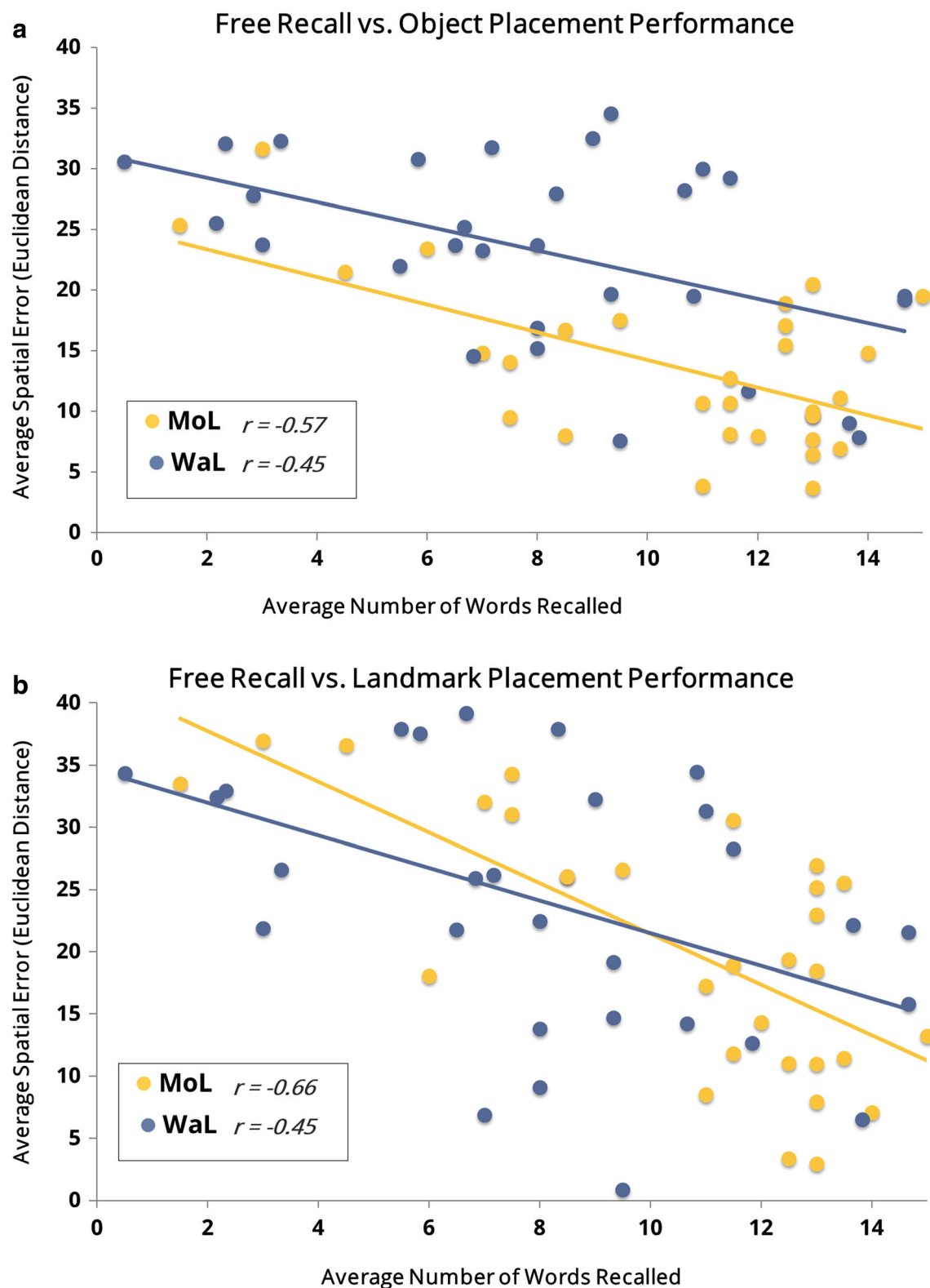


Fig. 8 Individual differences in free recall vs. allocentric memory performance. **a** Scatter plot depicting a participant's average number of words recalled across the three VEs (x-axis) vs. their average performance on the object-placement task (y-axis). **b** Scatter plot depicting a participant's average number of words recalled across the three VEs (x-

axis) vs. their average performance on the landmark-placement task (y-axis). Individual points are color-coded to reflect group membership. Trend lines indicate the linear trend across participants, respective of group, and are accompanied by r values and p values

Table 1 Relationship between free recall and spatial memory

		Object- placement	Landmark- placement	Coin- placement	Baseline spatial memory
Forward recall	Recall _{TOTAL}				
	MoL	-0.57***	-0.66**	-0.44*	0.11
	WaL	-0.45*	-0.45*	-0.35	0.18
	Recall _{CLUST}				
	MoL	-0.62***	-0.40	-0.08	0.01
	WaL	-0.34	-0.37	-0.26	0.23

R-statistics denoting the correlation between a participant's average free recall memory and their average performance on the placement tasks or baseline spatial-memory (reduction in time between first and second coin collection attempts) within the MoL ($n = 30$) or WaL ($n = 30$) groups. The Benjamini-Hochberg corrected p values are indicated as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

explanatory power [$F_{(4,52)} = 4.97$, $p = 0.002$]. Again, only the placement \times gender interaction revealed a significant coefficient [$t_{(58)} = -2.44$, $p = 0.02$], and the correlation between object-placement spatial memory and Reverse-Recall_{TOTAL} was lesser in males ($r = -0.39$, $p = 0.03$) than females ($r = -0.79$, $p < 0.001$)—a significant difference ($z = 2.47$, $p = 0.01$). Adding a participant's gender to a linear model of group and object-placement spatial memory on Recall_{CLUST} did not increase the model's explanatory power [$F_{(4,52)} = 1.68$, $p = 0.34$] neither did adding a participant's gender to a linear model of group and object-placement spatial memory on Reverse-Recall_{CLUST} [$F_{(4,52)} = 1.03$, $p = 0.40$]. While males recalled more words than females (10.27 vs. 8.42 average words recalled per list), this difference was only marginally significant [$F_{(1,59)} = 3.88$, $p = 0.05$].

Post-experimental Questionnaire

A participant's Presence_{SLATER} showed no correlation with Recall_{TOTAL} ($r = 0.13$, $p = 0.34$) and a participant's group assignment played no role in their score [$F_{(1,58)} = 1.24$, $p = 0.27$]. Presence_{FOX} also showed no relationship with Recall_{TOTAL} ($r = 0.09$, $p = 0.49$) and no effect of group [$F_{(1,58)} = 0.03$, $p = 0.86$]. In response to the questions "To what degree did you feel you were 'in' (Toon/Lagoon/Ruin) World as you moved around?", participants indicated equal immersion across all encoding environments [$F_{(2,177)} = 0.82$, $p = 0.44$]; there was no effect of group.

After the conclusion of the experiment, participants were asked to assess how confident they were that they would be able to recall the lists they just encoded if they were to be tested again in 24 h. Participants in the MoL group had higher confidence compared to WaL participants [$F_{(1,54)} = 5.12$, $p = 0.03$, $d = 0.60$]. This group effect went away when participants were asked about their confidence in a hypothetical recall test 1 week [$F_{(1,58)} = 3.12$, $p = 0.08$] or 1 month later [$F_{(1,57)} = 1.05$, $p = 0.31$]. Participants indicated whether or not they had heard of the method of loci/memory palace technique before taking part in this study. Previous exposure to the technique played no role in determining participant's Recall_{TOTAL} [$F_{(2,57)} = 0.14$, $p = 0.87$].

Discussion

In this study, we developed a novel VR-based platform that allowed participants to utilize a variant of the classic method of loci (MoL) mnemonic to support their memorization of arbitrary lists of information. Specifically, we challenged participants with the task of learning three sets of 15 objects, which were sequentially rendered in front of their avatar as they navigated at will through three different virtual worlds. With the precise experimental control afforded by the technology employed, this study sought to disentangle the various factors that could theoretically contribute to the efficacy of the MoL. Specifically, we tested whether or not the explicit binding of objects to the spatial environment was a major contributing factor to the MoL's ability to reliably increase memory strength. To accomplish this, participants were assigned to one of two groups. Participants in the MoL group were briefed on the use of the MoL mnemonic and given the ability to "freeze" each object in place at the location of their choosing. Participants in the Walk and Learn (WaL) group were informed that they would be utilizing a "proven" memory enhancement technique that exploited the principles of active learning, but they were not given the opportunity to freeze objects in place. Despite the fact that both groups encoded the object lists in the same VR contexts and had matched exposure to the objects, we found that the MoL group recalled an average of 27.9% more objects per list than their WaL counterparts. The advantage of the MoL group was magnified (33.7% better recall than WaL group) when participants were asked to recall the object lists in reverse order (i.e., starting with the last item encountered in each world).

In addition to having better overall recall of the object lists, participants in the MoL group also showed better allocentric spatial memory for the final location of each object within each environment when tested using a bird's-eye view map. However, the relationship between individual differences in recall and performance in the object-placement task within the MoL group was no stronger than that observed in the WaL group, suggesting that the effect of remembering where an object was in the environment is intimately related to the

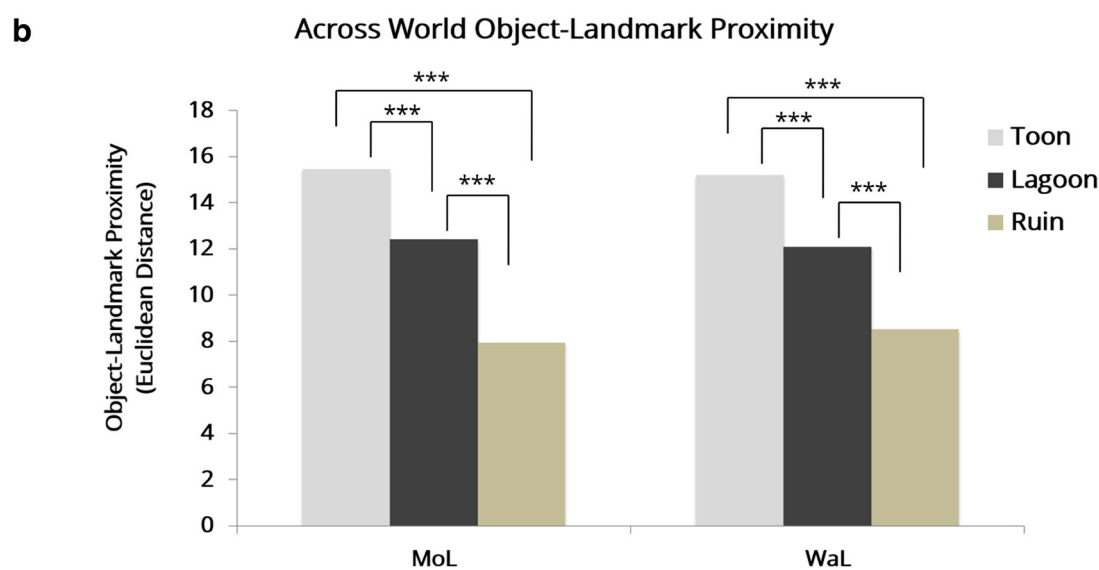
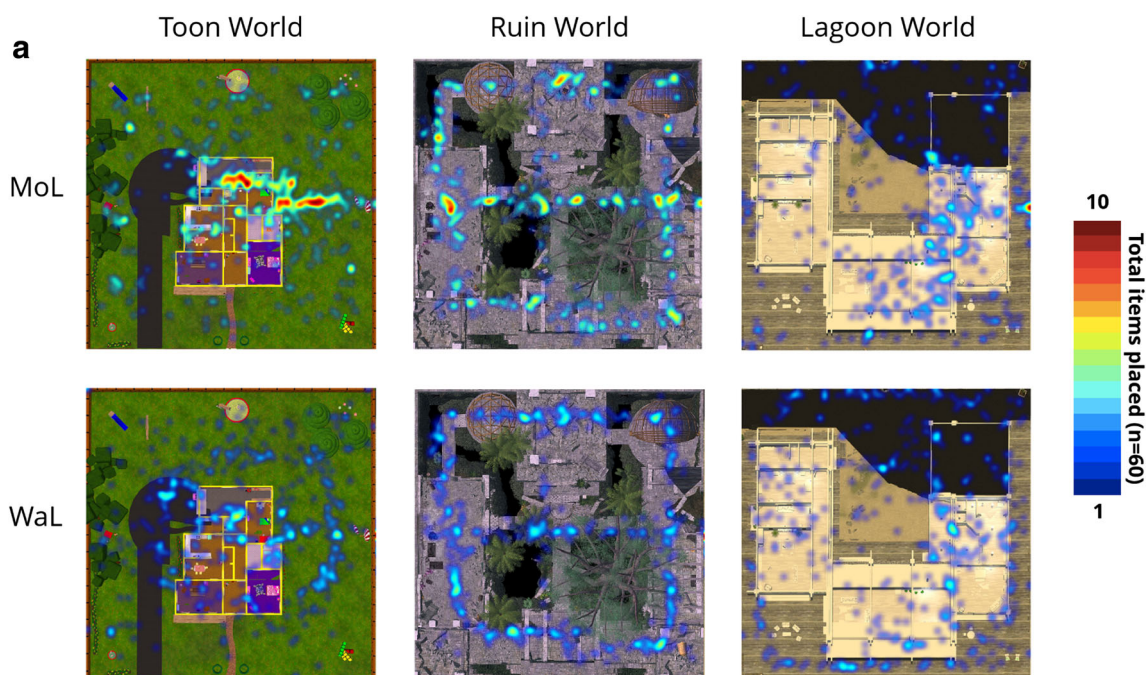


Fig. 9 Object-landmark proximity. **a** Heat map indicating the total number of objects placed by a group's participants within each cell of the 64×64 environmental grid, overlaid on a bird's-eye view of each VE.

b Average proximity of an object to the nearest environmental landmark (defined by Euclidean distance) as a function of encoding environment and group. *** $p < 0.001$

memory of the object itself, independent of group. Our finding that adding a participant's object-placement score to a linear model of group on recall significantly improved explanatory power strengthens this interpretation.

Since the MoL has traditionally been lauded for its ability to increase serially ordered recall, it is perhaps surprising that the significant effects of group membership on overall recall did not also extend to measures of participants' ability to recall the items in the correct temporal sequence. The two groups did not significantly differ in their degree of serial clustering

($\text{Recall}_{\text{CLUST}}$). Typically, a high serial clustering score goes hand in hand with improved overall recall ability (Fisher and Deluca 1997; Harnadek and Rourke 1994), putatively due to the strategic forging of associations between successive words during encoding. Although we do not have reports of participants' use of semantic binding strategies, it is reasonable to speculate that without the guidance of the MoL mnemonic, WaL participants defaulted to the intuitive technique of inter-item semantic binding, which could have diminished the difference in sequential recall performance across the two groups.

Crucially, it was not the case that participants with greater baseline spatial memory ability performed better on the object list recall task. Specifically, the two groups did not differ in their improvement between token-collection attempts nor on the token-placement memory tasks. Interestingly, performance on the landmark-placement memory task was related to a participant's overall object list recall ($\text{Recall}_{\text{TOTAL}}$). This could be reflective of the degree to which a participant was encoding the spatial arrangement of the environment in which they were encoding the to-be-remembered objects. To address the potential that participants were benefiting from an elaborative encoding of specific objects to landmarks in the environment, we analyzed for relationships between recall performance and the average proximity of objects to their nearest landmark. However, this analysis yielded no significant findings.

The impact of object-placement spatial memory on $\text{Recall}_{\text{TOTAL}}$ was strengthened when a participant's gender was taken into consideration. Specifically, adding a participant's gender to a linear model of group and object-placement spatial memory on $\text{Recall}_{\text{TOTAL}}$ significantly increased the model's explanatory power and yielded a sole significant coefficient: the interaction of gender and object-placement spatial memory. This finding suggests that gender and object-placement spatial memory were more potent predictors than group (i.e., MoL vs. WaL) in regard to recall strength, offering further support for our claims that spatial information is integral to the encoding process and extending previous work that reveals how males and females differ in spatial processing strategies and behavior (Astur et al. 2016; Lawton 1994; Persson et al. 2013; Sutcliffe et al. 2007). Our follow-up finding that females had a stronger relationship between object-placement spatial memory and recall compared to males could be a residual effect stemming from females' tendency to employ a landmark-based navigation strategy compared to the orientation strategy employed by males (Rahman et al. 2005; Sandstrom et al. 1998). If females tend to naturally orient themselves in space based on the presence of objects (i.e., landmarks), it follows that their recall for objects would be more closely tied to their spatial memory for the location of those objects.

Taken together, these findings add important empirical evidence to the conversation surrounding the primacy of spatial contexts in encoding (see Robin 2018) and the recruitment of spatial processing codes for cognition (Bellmund et al. 2018). Specifically, our findings that non-baseline assessments of spatial memory strength were predictive of recall strength, independent of encoding instructions, suggests that if one can forge a memory for an object within a spatial locus, there is a greater likelihood of that object being remembered. Given that the MoL mnemonic enforces precisely this object-location binding behavior during encoding, it should come as no surprise that MoL has been so historically effective and that removing this integral feature of the technique (i.e., no explicit placement/binding of objects to environmental loci, as in the WaL group) dramatically diminishes its effectiveness.

Limitations

A principal limitation of this study is the entanglement of both object-placement functionality and increased volitional control afforded only to the MoL group. Given that volitional control has been shown to benefit memory performance and upregulate encoding networks (Voss et al. 2011), it is possible that the MoL group's increased recall performance—an effect we posit is largely driven by the use of spatial memory as a scaffolding for object binding—could be partially explained by attentional enhancements due the decision processes inherent in search for and clicking on a memorable placement location for each object. That said, both the MoL and WaL groups were given complete freedom over where they could explore during encoding, which contrasts with prior work where a volitional control group was compared to a passive learning group (Voss et al. 2011). However, future research will be needed to more explicitly isolate the contributions of volitional control within a paradigm similar to that of the current study.

Another limitation is that recall was only tested immediately after an encoding period, and thus, we lack assessment of the long-term durability of the object list memories. Further investigations will be needed to elucidate the impacts of the MoL strategy on long-term retention; it could be the case that group differences in temporal order memory (as assessed by $\text{Recall}_{\text{CLUST}}$) would reach significance if more time passed between encoding and testing.

Finally, given recent work showing a comparable boost in recall when using spatially mediated (e.g., MoL) or temporally mediated (e.g., associating to-be-remembered information progressing along one's autobiographical timeline) encoding strategies compared to an uninstructed strategy (Bouffard et al. 2018), the current study missed an opportunity to tease apart temporal and spatial contributions. Future research using this virtual toolkit could consider including a third group where participants are given a series of experiences within a single spatial location and later go on to associate the to-be-remembered objects with each of the said experiences.

Future Directions

Given the technological affordances of modern life, humans have a reduced imperative to become skilled at rapidly memorizing lists of objects rapidly. After all, why should one bother to create a memory palace for storing today's list of groceries when it is probably easier, more reliable, and less time consuming to create a checklist on one's smartphone phone or notepad? In fact, despite the widespread knowledge of the MoL technique's effectiveness, most learners admit to never using the technique—even when explicitly instructed to do so in an experiment (Legge et al. 2012). Undergraduate students even report their lack of use of mnemonic strategies, despite

their knowledge of their effectiveness (Susser and McCabe 2013). The most common strategy amongst undergraduates for studying is still rote repetition (Karpicke et al. 2009).

The once revered “art of memory” seems to now only be reserved for a small niche of memory enthusiasts who practice mnemonic techniques for relatively useless, albeit impressive, personal goals (e.g., memorizing Pi out to thousands of decimal places) or understandably motivating competitive reasons (e.g., the World Memory Championship carries a \$30,000 prize; Foer 2011). However, the reliable effectiveness of the MoL, and the evolutionarily honed spatial binding mechanisms that it leverages, needs not be limited to increasing the recall of arbitrary lists of digits or words. While further research will be needed to verify the possibility of extending the technique beyond list learning, one can speculate on the ability for spatial strategies to bolster recall for procedural, conceptual, and episodic memory—all aspects of human cognition that cannot as easily be offloaded to a computer. While it has been suggested that mnemonics are limited in applicability and do not conform to theory or structure of general memory, emerging concepts which emphasize the primacy of spatial constructs for the encoding of events (Mullally and Maguire 2014; Robin 2018) permit for novel and creative ways to utilize space to both operate on and retain information.

Encoding information within a spatial scaffolding is also ripe for the incidental insertion of additional information. For instance, a learner could navigate about a virtual room that contains only a large elephant and then move through a doorway into another room where a monkey is opening the passenger door of a car that has 2 balloons tied to it. The learner could later be instructed to mentally traverse this memorable path and write down the first letter of each object they encounter, with the simple instructions to insert an equal sign whenever they pass through a door and exponents whenever they see balloons. By simply recalling this scene, the learner could incidentally unveil a “memory” for $E = MC^2$. Similar, seemingly abstract concepts (e.g., fractions) also stand to benefit from spatially based incidental encoding tricks (e.g., floors separating numerators and denominators). Extending the MoL in ways where it can permit for the encoding of information beyond just that of lists of objects is of high importance when considering the broader educational impacts.

Additionally, the MoL has even been utilized for therapeutic purposes: researchers have increased the recall of self-affirming memories and coping protocols for individuals with depression (Dalglish et al. 2013; Werner-Seidler and Dalglish 2016) and provided an aid for both aging (Rapp et al. 2002; Verhaeghen et al. 1992; West 1995; Yesavage 1983) and memory-impaired populations (Richardson 1995; Tate 1997). Our VR-based paradigm significantly decreases the extensive training that is typically necessary to teach users to implement the MoL technique (Bower and Reitman 1972; Brehmer et al. 2008; Brooks et al. 1993; Kliegl et al. 1990;

Moè and De Beni 2005). As such, our VR procedure could be adapted as a tool to introduce memory-impaired patients about the MoL technique and to convince them of its effectiveness, leading them to be more likely to implement this mnemonic in their everyday lives to help remember important information.

Acknowledgments The authors of this project extend an enormous gratitude to Forde “JubJub” Davidson for his countless hours of virtual scripting and design, without which this current work would not have been possible. A thanks is also sent to Majed Samad, Ph.D., for his assistance with creating PsychToolbox testing materials and to John Dell’Italia for guidance on statistical analyses.

Funding Information This work was supported by a Defense Advanced Research Project Agency (DARPA) Research Grant awarded to J.R. (D13AP00057) and National Science Foundation (NSF) Graduate Research Fellowships awarded to N.R. (DGE-1650604) and J.K.-Y.E. (DGE-1144087).

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

References

- Astur, R. S., Purton, A. J., Zaniewski, M. J., Cimadevilla, J., & Markus, E. J. (2016). Human sex differences in solving a virtual navigation problem. *Behavioural Brain Research*, 308, 236–243. <https://doi.org/10.1016/j.bbr.2016.04.037>.
- Balch, W. R. (2005). Elaborations of introductory psychology terms: effects on test performance and subjective ratings. *Teaching of Psychology*, 32, 29–34.
- Bandura, A. (1993). Perceived self-efficacy in cognitive development and functioning. *Educational Psychologist*, 28, 117–148. https://doi.org/10.1207/s15326985ep2802_3.
- Bellmund, J. L. S., Gärdenfors, P., Moser, E. I., & Doeller, C. F. (2018). Navigating cognition: spatial codes for human thinking. *Science*, 362, eaat6766. <https://doi.org/10.1126/science.aat6766>.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B: Methodological*, 57, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>.
- Benn, Y., Bergman, O., Glazer, L., Arent, P., Wilkinson, I. D., Varley, R., et al. (2015). Navigating through digital folders uses the same brain structures as real world navigation. *Scientific Reports*, 5, 14719. <https://doi.org/10.1038/srep14719>.
- Bjork, R. A. (1994). Memory and metamemory considerations in the training of human beings. In J. Metcalfe & A. P. Shimamura (Eds.), *Metacognition Knowing about knowing*, (pp 185–205). Cambridge: The MIT Press.
- Black, J. B., Turner, T. J., & Bower, G. H. (1979). Point of view in narrative comprehension, memory, and production. *Journal of Verbal Learning and Verbal Behavior*, 18, 187–198. [https://doi.org/10.1016/S0022-5371\(79\)90118-X](https://doi.org/10.1016/S0022-5371(79)90118-X).
- Bouffard, N., Stokes, J., Kramer, H. J., & Ekstrom, A. D. (2018). Temporal encoding strategies result in boosts to final free recall performance comparable to spatial ones. *Memory & Cognition*, 46, 17–31. <https://doi.org/10.3758/s13421-017-0742-z>.

- Bower, G. H. (1970). Analysis of a mnemonic device: modern psychology uncovers the powerful components of an ancient system for improving memory. *American Scientist*, 58, 496–510.
- Bower, G. H., & Reitman, J. S. (1972). Mnemonic elaboration in multilist learning. *Journal of Verbal Learning and Verbal Behavior*, 11, 478–485.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- Brehmer, Y., Li, S.-C., Straube, B., Stoll, G., von Oertzen, T., Müller, V., et al. (2008). Comparing memory skill maintenance across the life span: preservation in adults, increase in children. *Psychology and Aging*, 23, 227.
- Briggs, G. G., Hawkins, S., & Crovitz, H. F. (1970). Bizarre images in artificial memory. *Psychonomic Science*, 19, 353–354. <https://doi.org/10.3758/BF03328856>.
- Brooks, J. O., Friedman, L., & Yesavage, J. A. (1993). A study of the problems older adults encounter when using a mnemonic technique. *International Psychogeriatrics*, 5, 57–65.
- Bush, D., Barry, C., Manson, D., & Burgess, N. (2015). Using grid cells for navigation. *Neuron*, 87, 507–520. <https://doi.org/10.1016/j.neuron.2015.07.006>.
- Carney, R. N., & Levin, J. R. (1998). Mnemonic strategies for adult learners. In M. C. Smith & T. Pourchot (Eds.), *Adult Learning and Development: Perspectives from Educational Psychology*, (pp 159–175). Mahwah: Lawrence Erlbaum Associates Publishers.
- Chen, H.-Y., Gilmore, A. W., Nelson, S. M., & McDermott, K. B. (2017). Are there multiple kinds of episodic memory? An fMRI investigation comparing autobiographical and recognition memory tasks. *Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 37, 2764–2775. <https://doi.org/10.1523/JNEUROSCI.1534-16.2017>.
- Cohen, J., & Cohen, J. (2003). In N. J. Mahwah (Ed.), *Applied multiple regression/correlation analysis for the behavioral sciences*. Mahwah: L. Erlbaum Associates.
- Constantinescu, A. O., O'Reilly, J. X., & Behrens, T. E. (2016). Organizing conceptual knowledge in humans with a gridlike code. *Science*, 352, 1464–1468.
- Crovitz, H. F. (1971). The capacity of memory loci in artificial memory. *Psychonomic Science*, 24, 187–188. <https://doi.org/10.3758/BF03335561>.
- Cui, X., Jeter, C. B., Yang, D., Montague, P. R., & Eagleman, D. M. (2007). Vividness of mental imagery: individual variability can be measured objectively. *Vision Research*, 47, 474–478. <https://doi.org/10.1016/j.visres.2006.11.013>.
- Dalglish, T., Navrady, L., Bird, E., Hill, E., Dunn, B. D., & Golden, A.-M. (2013). Method-of-loci as a mnemonic device to facilitate access to self-affirming personal memories for individuals with depression. *Clinical Psychological Science: A Journal of the Association for Psychological Science*, 1, 156–162. <https://doi.org/10.1177/2167702612468111>.
- Dennett, D. C. (1993). Consciousness explained. In *Penguin Adult*.
- Eichenbaum, H. (2004). Hippocampus: cognitive processes and neural representations that underlie declarative memory. *Neuron*, 44, 109–120. <https://doi.org/10.1016/j.neuron.2004.08.028>.
- Eichenbaum, H., & Cohen, N. J. (2014). Can we reconcile the declarative memory and spatial navigation views on hippocampal function? *Neuron*, 83, 764–770.
- Ericsson, K. A., & Kintsch, W. (1995). Long-term working memory. *Psychological Review*, 102, 211.
- Ericsson, K. A., Cheng, X., Pan, Y., Ku, Y., Ge, Y., & Hu, Y. (2017). Memory skills mediating superior memory in a world-class memorist. *Memory*, 25, 1294–1302. <https://doi.org/10.1080/09658211.2017.1296164>.
- Fellner, M.-C., Volberg, G., Wimber, M., Goldhacker, M., Greenlee, M. W., & Hanslmayr, S. (2016). Spatial mnemonic encoding: theta power decreases and medial temporal lobe BOLD increases occur during the usage of the method of loci. *eNeuro*, 3. <https://doi.org/10.1523/ENEURO.0184-16.2016>.
- Fisher, N. J., & Deluca, J. W. (1997). Verbal learning strategies of adolescents and adults with the syndrome of nonverbal learning disabilities. *Child Neuropsychology*, 3, 192–198. <https://doi.org/10.1080/09297049708400642>.
- Foer, J. (2011). *Moonwalking with Einstein: the art and science of remembering everything*. New York: Penguin Press.
- Fox, J., Bailenson, J., & Binney, J. (2009). Virtual experiences, physical behaviors: the effect of presence on imitation of an eating avatar. *Presence Teleoperators Virtual Environ.*, 18, 294–303. <https://doi.org/10.1162/pres.18.4.294>.
- Hafting, T., Fyhn, M., Molden, S., Moser, M.-B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, 436, 801–806. <https://doi.org/10.1038/nature03721>.
- Hamann, S. (2001). Cognitive and neural mechanisms of emotional memory. *Trends in Cognitive Sciences*, 5, 394–400. [https://doi.org/10.1016/S1364-6613\(00\)01707-1](https://doi.org/10.1016/S1364-6613(00)01707-1).
- Harnadek, M. C., & Rourke, B. P. (1994). Principal identifying features of the syndrome of nonverbal learning disabilities in children. *Journal of Learning Disabilities*, 27, 144–154. <https://doi.org/10.1177/002221949402700303>.
- Harris, P. A., Taylor, R., Thielke, R., Payne, J., Gonzalez, N., & Conde, J. G. (2009). Research Electronic Data Capture (REDCap)—a metadata-driven methodology and workflow process for providing translational research informatics support. *Journal of Biomedical Informatics*, 42, 377–381. <https://doi.org/10.1016/j.jbi.2008.08.010>.
- Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with construction. *Trends in Cognitive Sciences*, 11, 299–306.
- Hassabis, D., & Maguire, E. A. (2009). The construction system of the brain. *Philosophical Transactions of the Royal Society B Biological Sciences*, 364, 1263–1271.
- Hebscher, M., Levine, B., & Gilboa, A. (2017). The precuneus and hippocampus contribute to individual differences in the unfolding of spatial representations during episodic autobiographical memory. *Neuropsychologia*, 110, 123–133. Chicago.
- Herrmann, D. J., Geisler, F. V., & Atkinson, R. C. (1973). The serial position function for lists learned by a narrative-story mnemonic. *Bulletin of the Psychonomic Society*, 2, 377–378. <https://doi.org/10.3758/BF03334418>.
- Horner, A. J., Bisby, J. A., Wang, A., Bogus, K., & Burgess, N. (2016). The role of spatial boundaries in shaping long-term event representations. *Cognition*, 154, 151–164.
- Hu, Y., & Ericsson, K. A. (2012). Memorization and recall of very long lists accounted for within the long-term working memory framework. *Cognitive Psychology*, 64, 235–266.
- Hu, Y., Ericsson, K. A., Yang, D., & Lu, C. (2009). Superior self-paced memorization of digits in spite of a normal digit span: the structure of a memorist's skill. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 35, 1426.
- Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: the parallel map theory of hippocampal function. *Psychological Review*, 110, 285–315. <https://doi.org/10.1037/0033-295X.110.2.285>.
- Karpicke, J. D., Butler, A. C., & Roediger, H. L., III. (2009). Metacognitive strategies in student learning: do students practise retrieval when they study on their own? *Memory*, 17, 471–479.
- Kliegl, R., Smith, J., & Baltes, P. B. (1990). On the locus and process of magnification of age differences during mnemonic training. *Developmental Psychology*, 26, 894.
- Kondo, Y., Suzuki, M., Mugikura, S., Abe, N., Takahashi, S., Iijima, T., et al. (2005). Changes in brain activation associated with use of a memory strategy: a functional MRI study. *NeuroImage*, 24, 1154–1163. <https://doi.org/10.1016/j.neuroimage.2004.10.033>.
- Kosslyn, S. M., Brunn, J., Cave, K. R., & Wallach, R. W. (1984). Individual differences in mental imagery ability: a computational

- analysis. *Cognition*, 18, 195–243. [https://doi.org/10.1016/0010-0277\(84\)90025-8](https://doi.org/10.1016/0010-0277(84)90025-8).
- Lawton, C. A. (1994). Gender differences in way-finding strategies: relationship to spatial ability and spatial anxiety. *Sex Roles*, 30, 765–779.
- Lee, I. A., & Preacher, K. J. (2013). *Calculation for the test of the difference between two dependent correlations with one variable in common*. Available at: <http://quantpsy.org>. Accessed March 18 2018.
- Legge, E. L. G., Madan, C. R., Ng, E. T., & Caplan, J. B. (2012). Building a memory palace in minutes: equivalent memory performance using virtual versus conventional environments with the method of loci. *Acta Psychologica*, 141, 380–390. <https://doi.org/10.1016/j.actpsy.2012.09.002>.
- Levin, J. R. (1983). Pictorial strategies for school learning: practical illustrations. In *Cognitive Strategy Research Springer Series in Cognitive Development* (pp. 213–237). New York, NY: Springer. https://doi.org/10.1007/978-1-4612-5519-2_8.
- Llinás, R. R. (2001). *I of the vortex: from neurons to self*. Cambridge, MA: MIT press.
- Llinas, R., & Ribary, U. (2001). Consciousness and the brain. *Annals of the New York Academy of Sciences*, 929, 166–175.
- Maguire, E. A., & Mullally, S. L. (2013). The Hippocampus: a manifesto for change. *Journal of Experimental Psychology: General*, 142, 1180–1189. <https://doi.org/10.1037/a0033650>.
- Maguire, E. A., Valentine, E. R., Wilding, J. M., & Kapur, N. (2003). Routes to remembering: the brains behind superior memory. *Nature Neuroscience*, 6, 90.
- Martell, R. F., & Willis, C. E. (1993). Effects of observers' performance expectations on behavior ratings of work groups: memory or response bias? *Organizational Behavior and Human Decision Processes*, 56, 91–109. <https://doi.org/10.1006/obhd.1993.1046>.
- McCabe, J. A. (2015). Location, location, location! Demonstrating the mnemonic benefit of the method of loci. *Teaching of Psychology*, 42, 169–173. <https://doi.org/10.1177/0098628315573143>.
- McCabe, J. A., Osha, K. L., Roche, J. A., & Susser, J. A. (2013). Psychology students' knowledge and use of mnemonics. *Teaching of Psychology*, 40, 183–192.
- Merriman, N. A., Ondřej, J., Roudaia, E., O'Sullivan, C., & Newell, F. N. (2016). Familiar environments enhance object and spatial memory in both younger and older adults. *Experimental Brain Research*, 234, 1555–1574.
- Moè, A., & De Beni, R. (2005). Stressing the efficacy of the loci method: oral presentation and the subject-generation of the loci pathway with expository passages. *Applied Cognitive Psychology*, 19, 95–106.
- Moscovitch, M., Cabeza, R., Winocur, G., & Nadel, L. (2016). Episodic memory and beyond: the hippocampus and neocortex in transformation. *Annual Review of Psychology*, 67, 105–134.
- Mullally, S. L., & Maguire, E. A. (2014). Memory, imagination, and predicting the future: a common brain mechanism? *The Neuroscientist*, 20, 220–234. <https://doi.org/10.1177/1073858413495091>.
- Murray, E. A., Wise, S. P., & Graham, K. S. (2018). Representational specializations of the hippocampus in phylogenetic perspective. *Neuroscience Letters*, 680, 4–12. <https://doi.org/10.1016/j.neulet.2017.04.065>.
- Nelson, D. L., Reed, V. S., & Walling, J. R. (1976). Pictorial superiority effect. *Journal of Experimental Psychology [Human Learning and Memory]*, 2, 523–528.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Oxford University Press.
- Paivio, A., & Csapo, K. (1973). Picture superiority in free recall: imagery or dual coding? *Cognitive Psychology*, 5, 176–206. [https://doi.org/10.1016/0010-0285\(73\)90032-7](https://doi.org/10.1016/0010-0285(73)90032-7).
- Persson, J., Herlitz, A., Engman, J., Morell, A., Sjölie, D., Wikström, J., et al. (2013). Remembering our origin: gender differences in spatial memory are reflected in gender differences in hippocampal lateralization. *Behavioural Brain Research*, 256, 219–228. <https://doi.org/10.1016/j.bbr.2013.07.050>.
- Preacher, K. J. (2002). *Calculation for the test of the difference between two independent correlation coefficients*. Available at: <http://quantpsy.org>. Accessed March 18, 2018.
- Pyc, M. A., & Rawson, K. A. (2009). Testing the retrieval effort hypothesis: does greater difficulty correctly recalling information lead to higher levels of memory? *Journal of Memory and Language*, 60, 437–447. <https://doi.org/10.1016/j.jml.2009.01.004>.
- Qureshi, A., Rizvi, F., Syed, A., Shahid, A., & Manzoor, H. (2014). The method of loci as a mnemonic device to facilitate learning in endocrinology leads to improvement in student performance as measured by assessments. *Advances in Physiology Education*, 38, 140–144. <https://doi.org/10.1152/advan.00092.2013>.
- R Core Team. (2013). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing Available at: <http://www.R-project.org/>.
- Rahman, Q., Andersson, D., & Govier, E. (2005). A specific sexual orientation-related difference in navigation strategy. *Behavioral Neuroscience*, 119, 311–316. <https://doi.org/10.1037/0735-7044.119.1.311>.
- Rapp, S., Brenes, G., & Marsh, A. P. (2002). Memory enhancement training for older adults with mild cognitive impairment: a preliminary study. *Aging & Mental Health*, 6, (1), 5–11. <https://doi.org/10.1080/13607860120101077>.
- Reggente, N., Essoe, J. K.-Y., Aghajan, Z. M., Tavakoli, A. V., McGuire, J. F., Suthana, N. A., et al. (2018). Enhancing the ecological validity of fMRI memory research using virtual reality. *Frontiers in Neuroscience*, 12. <https://doi.org/10.3389/fnins.2018.00408>.
- Richardson, J. T. (1995). The efficacy of imagery mnemonics in memory remediation. *Neuropsychologia*, 33, 1345–1357.
- Rissman, J., & Wagner, A. D. (2012). Distributed representations in memory: insights from functional brain imaging. *Annual Review of Psychology*, 63, 101–128. <https://doi.org/10.1146/annurev-psych-120710-100344>.
- Robin, J. (2018). Spatial scaffold effects in event memory and imagination. *Wiley Interdisciplinary Reviews: Cognitive Science*, 9, e1462. <https://doi.org/10.1002/wcs.1462>.
- Robin, J., Wynn, J., & Moscovitch, M. (2016). The spatial scaffold: the effects of spatial context on memory for events. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 42, 308.
- Robin, J., Buchsbaum, B. R., & Moscovitch, M. (2018). The primacy of spatial context in the neural representation of events. *Journal of Neuroscience: The Official Journal of the Society for Neuroscience*. <https://doi.org/10.1523/JNEUROSCI.1638-17.2018>.
- Roediger, H. L. (1980). The effectiveness of four mnemonics in ordering recall. *Journal of Experimental Psychology [Human Learning]*, 6, 558–567. <https://doi.org/10.1037/0278-7393.6.5.558>.
- Rogers, T. B., Kuiper, N. A., & Kirker, W. S. (1977). Self-reference and the encoding of personal information. *Journal of Personality and Social Psychology*, 35, 677.
- Ross, J., & Lawrence, K. A. (1968). Some observations on memory artifice. *Psychonomic Science*, 13, 107–108. <https://doi.org/10.3758/BF03342433>.
- Rummel, J., & Meiser, T. (2013). The role of metacognition in prospective memory: anticipated task demands influence attention allocation strategies. *Consciousness and Cognition*, 22, 931–943. <https://doi.org/10.1016/j.concog.2013.06.006>.
- Sandstrom, N. J., Kaufman, J., & Huettel, S. A. (1998). Males and females use different distal cues in a virtual environment navigation task. *Brain Research. Cognitive Brain Research*, 6, 351–360.
- Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, 20, 11–21.
- Shimamura, A. P. (1984). A guide for teaching mnemonic skills. *Teaching of Psychology*, 11, 162–166.

- Slater, M., Usoh, M., & Steed, A. (1994). Depth of presence in virtual environments. *Presence Teleoperators and Virtual Environments*, 3, 130–144. <https://doi.org/10.1162/pres.1994.3.2.130>.
- Slater, M., Usoh, M., & Chrysanthou, Y. (1995a). The influence of dynamic shadows on presence in immersive virtual environments. In *Virtual environments '95* (pp. 8–21). Berlin: Springer.
- Slater, M., Usoh, M., & Steed, A. (1995b). Taking steps: the influence of a walking technique on presence in virtual reality. *ACM Transactions on Computer-Human Interaction TOCHI*, 2, 201–219.
- Slater, M., McCarthy, J., & Maringelli, F. (1998). The influence of body movement on subjective presence in virtual environments. *Human Factors*, 40, 469–477.
- Squire, L. R. (1992). Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychological Review*, 99, 195–231.
- Squire, L. R., & Zola, S. M. (1996). Structure and function of declarative and nondeclarative memory systems. *Proceedings of the National Academy of Sciences of the United States of America*, 93, 13515–13522.
- Steiger, J. H. (1980). Tests for comparing elements of a correlation matrix. *Psychological Bulletin*, 87, 245–251. <https://doi.org/10.1037/0033-2909.87.2.245>.
- Stricker, J. L., Brown, G. G., Wixted, J., Baldo, J. V., & Delis, D. C. (2002). New semantic and serial clustering indices for the California Verbal Learning Test-Second Edition: background, rationale, and formulae. *Journal of the International Neuropsychological Society JINS*, 8, 425–435.
- Susser, J. A., & McCabe, J. (2013). From the lab to the dorm room: metacognitive awareness and use of spaced study. *Instructional Science*, 41, 345–363.
- Sutcliffe, J. S., Marshall, K. M., & Neill, J. C. (2007). Influence of gender on working and spatial memory in the novel object recognition task in the rat. *Behavioural Brain Research*, 177, 117–125.
- Tate, R. L. (1997). Subject review: beyond one-bun, two-shoe: recent advances in the psychological rehabilitation of memory disorders after acquired brain injury. *Brain Injury*, 11, 907–918.
- The Mathworks, Inc. (2012). *MATLAB and Statistics Toolbox*. Natick, Massachusetts, United States.
- Tulving, E. (2002). Episodic memory: from mind to brain. *Annual Review of Psychology*, 53, 1–25.
- Tulving, E., & Markowitsch, H. J. (1998). Episodic and declarative memory: role of the hippocampus. *Hippocampus*, 8, 198–204. [https://doi.org/10.1002/\(SICI\)1098-1063\(1998\)8:3<198::AID-HIPO2>3.0.CO;2-G](https://doi.org/10.1002/(SICI)1098-1063(1998)8:3<198::AID-HIPO2>3.0.CO;2-G).
- Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W., & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science*, 277, 376–380.
- Verhaeghen, P., Marcoen, A., & Goossens, L. (1992). Improving memory performance in the aged through mnemonic training: a meta-analytic study. *Psychology and Aging*, 7, 242.
- Voss, J. L., Gonsalves, B. D., Federmeier, K. D., Tranel, D., & Cohen, N. J. (2011). Hippocampal brain-network coordination during volitional exploratory behavior enhances learning. *Nature Neuroscience*, 14, 115. <https://doi.org/10.1038/nn.2693>.
- Werner-Seidler, A., & Dalgleish, T. (2016). The method of loci improves longer-term retention of self-affirming memories and facilitates access to mood-repairing memories in recurrent depression. *Clinical Psychological Science: A Journal of the Association for Psychological Science*, 4, 1065–1072. <https://doi.org/10.1177/2167702615626693>.
- West, R. L. (1995). Compensatory strategies for age-associated memory impairment. In A. D. Baddeley, B. A. Wilson, & F. N. Watts (Eds.), *Handbook of memory disorders* (pp. 481–500). Oxford, England: John Wiley & Sons.
- Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, 3, 1212–1217. <https://doi.org/10.1038/81497>.
- Yates, F. A. (1966). *The art of memory* (6th ed.). Chicago: University of Chicago Press.
- Yesavage, J. A. (1983). Imagery pretraining and memory training in the elderly. *Gerontology*, 29, 271–275.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.