Age differences in spatial memory are mitigated during naturalistic navigation

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Abstract

Spatial navigation deficits in older adults are well documented. These findings are based on experimental paradigms that require using a joystick or keyboard to navigate a virtual desktop environment. In the present study, cognitively normal young and older adults navigated in each of two virtual reality (VR) conditions: a desktop VR condition which required using a mouse and keyboard to navigate and an immersive and ambulatory VR condition which permitted unrestricted locomotion. Consistent with past studies, older adults navigated to target locations less precisely than did younger individuals in the desktop condition. These age differences were significantly attenuated when tested in the immersive environment. Additional analyses indicated that older adults showed a preference for route-based search strategies compared to young adults, regardless of condition. These findings suggest that certain aspects of navigation performance in older adults are improved in paradigms that offer a fuller range of enriched and naturalistic cues.

Keywords: spatial cognition, aging, navigation, learning, memory, virtual reality

Declines in spatial navigation as part of healthy aging are well documented, suggesting a strong relationship between advanced age and an impaired ability to remember spatial locations. Much of the early experimental work on spatial navigation in aging humans comes from studies employing virtual adaptations of the Morris water maze (vMWM) task. A common finding from these studies is that spatial memory deficits identified in older adults can be attributed to a selective failure to encode allocentric spatial representations of the environment using distal cues located outside of the search area[1–6]. Similar age-related differences in spatial abilities have also been observed in large-scale samples using experimental paradigms delivered on mobile-based gaming apps[7]. The findings from these studies have played a significant role in shaping current models of aging and spatial navigation[8–10].

Most studies employing the vMWM task to examine navigation deficits in aging humans have relied on experimental paradigms that require using a keyboard or joystick to navigate a virtual desktop environment. Consequently, the results of these desktop-based studies may be confounded by age differences in prior experience with computer gaming equipment and fine motor control related to joystick and keyboard use. Specifically, older adults may be at a comparative disadvantage due to less exposure to computers and desktop virtual reality (VR) compared to younger cohorts[11]. These findings raise the possibility that age differences in spatial navigation may be exaggerated in less familiar virtual desktop environments.

Experimental paradigms employing desktop-based VR also lack the type of naturalistic movements and self-generated idiothetic cues (e.g., proprioceptive, vestibular) that can help form complex spatial representations of the environment[12–14]. In an early study by Allen and colleagues (2004), older adults were observed to make more errors on a path integration task compared to younger individuals during trials in which only visual cues were available to navigate[15]. Young and older adults performed similarly on trials in which proprioceptive and vestibular sensory feedback was available, suggesting that spatial performance might be affected by the presence of multimodal sensory information (see also [16]). Yu and colleagues (2021) found that, compared to younger individuals, middle-aged adults were significantly impaired in their wayfinding abilities and took fewer shortcuts when navigating a desktop-VR maze[17]. The two age groups did not differ, however, on an immersive path integration task which, unlike the desktop-VR maze, provided both visual and proprioceptive feedback. Notably, these experiments focused specifically on path integration, which is particularly reliant on precise self-motion feedback.

Performance on the vMWM may be impaired in older relative to younger adults regardless of the availability of self-motion cues, suggesting a general age-related impairment on the task. Alternatively, older adults might be selectively impaired when using a keyboard and mouse to navigate a virtual desktop environment due to a combination of sensorimotor deficits and/or lack of computer experience. To address these possibilities, we compared spatial memory performance in cognitively healthy young and older adult humans as they navigated a virtual MWM adapted from McAvan et al. (2021)[18] in each of two conditions: 1) a desktop VR condition that required using a keyboard and mouse to navigate, and 2) an immersive VR condition in which participants wore a wireless head-mounted display that permitted unrestricted locomotion and self-generated idiothetic feedback during navigation. This allowed us to test competing hypotheses about the basis of navigation deficits in older compared to younger adults.

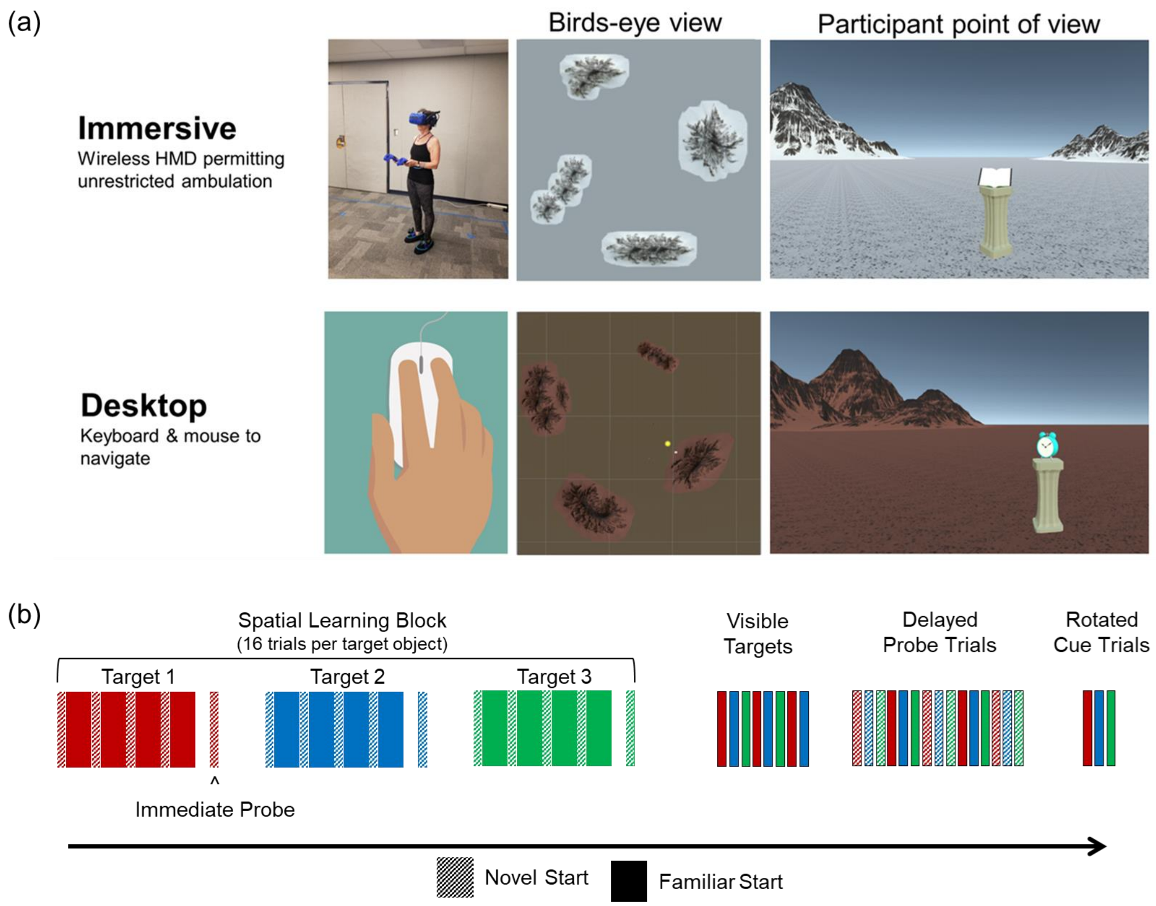

Figure 1. Virtual Morris Water Maze Task Design. (a) Visual depiction of the immersive and desktop VR conditions. The assignment of the respective environments (snow, desert) to each VR condition (desktop, immersive) was fully counterbalanced across participants, as was the testing order of the respective conditions. (b) During the spatial learning blocks, participants were trained to locate the spatial positions of three hidden target objects (color coded). Immediately following each spatial learning block participants were cued to recall the location of the hidden object without feedback (immediate probe trials). Following the learning blocks, participants completed eight visible target trials to rule out potential age-related motivational and/or sensorimotor confounds. Participants completed 12 delayed probe trials without feedback, during which they were cued to locate the hidden target when starting from a familiar (solid bars) or novel (dashed bars) viewpoint. In a subset of the delayed probe trials, a singular mountain cue was rotated 20 degrees clockwise or counterclockwise unbeknownst to the participant.

Results

Participants were trained to find the locations of hidden target objects in a virtual outdoor environment with four distal mountain cues visible outside of the navigable space (Figure 1). After completing three initial spatial learning blocks, participants were tested on their immediate and delayed recall of the hidden target locations (i.e., probe trials). During the delayed probe trials, we experimentally manipulated the relative familiarity of the navigation start positions to test predictions regarding age differences in the ability to switch between putative allocentric and egocentric spatial reference frames[18]. In a separate subset of the probe trials, we rotated the position of a singular mountain cue to assess potential age differences in the relative weighting of the distal cues during navigation.

Our principal objective was to examine the effect of age and VR condition on spatial memory assessed during the immediate and delayed probe trials. Results for the visible target trials are described further in the supplemental materials. Unless otherwise specified, we report the results of two-way mixed-factorial ANOVAs with factors of age group (young, older) and VR condition (desktop, immersive). Descriptive statistics for the primary outcome measures are summarized in Table 1.

Table 1. Mean (with standard deviation) of the primary outcome measures for each age group and VR condition.

	Desktop		Immersive				
	YA	OA	YA	OA	Age	Condition	Age x Condition
Median Distance Error (m)							
Spatial Learning	1.93 (1.11)	3.50 (.77)	1.76 (.49)	2.52 (.66)	***	***	**
Immediate Probe	1.73 (1.30)	3.32 (1.14)	2.05 (.73)	2.56 (.92)	***	*ns*	**
Delayed Probe	2.19 (1.54)	3.57 (.77)	2.45 (.93)	2.81 (.51)	**	*ns*	**
Delayed Probe Novel Start	2.76 (1.50)	3.82 (.63)	2.45 (.91)	3.04 (.57)	-	-	-
Delayed Probe Familiar Start	2.31 (1.54)	3.01 (.64)	2.20 (1.02)	2.56 (.40)	-	-	-
Response Time (ms)							
Immediate	19599 (13517)	25486 (34066)	25510 (14119)	15520 (8884)	*ns*	*ns*	**
Delayed	14615 (9809)	8128 (5922)	18702 (9558)	10959 (6505)	**	***	*ns*
Rotated Mountain Index	.60 (.22)	.47 (.11)	.55 (.13)	.49 (.10)	***	*ns*	*ns*
Rayleigh's Test of Uniformity	.21***	.22***	.20***	.12*	-	-	-

$^*p < .05$; $^{**} p < .01$; $^{***} p < .001$; YA = young adult, OA = older adult

Age differences in spatial precision are moderated by VR modality

Spatial precision was operationalized as the Euclidean distance (in virtual meters) between the remembered and true location of each target object (i.e., distance error). During the initial spatial learning trials (Figure 2A), we found a significant interaction between age group and VR condition ($F_{(1,38)} = 16.62$, $p = 2.25^{-4}$, partial-$\eta^2 = .304$, $BF_{10} = 7.727$). This interaction was driven by significantly greater distance error in the desktop compared to immersive condition in older adults ($t_{(38)} = 5.01$, $p < .001$, $BF_{10} = 1242.761$), but no significant difference between the respective conditions in young adults ($t_{(38)} = 0.87$, $p = .392$, $BF_{10} = 0.306$). Spatial precision was significantly reduced in older adults relative to younger individuals in both the desktop and immersive VR conditions ($t_{(38)} = 5.19$, $p < .001$, $BF_{10} = 2117.985$; $t_{(38)} = 4.10$, $p < .001$, $BF_{10} = 115.871$, respectively).

A similar interaction between age group and VR condition was also evident during the immediate ($F_{(1,38)} = 8.05$, $p = .007$, partial-$\eta^2 = .175$, $BF_{10} = 7.012$; Figure 2B) and delayed ($F_{(1,38)} = 7.87$, $p = .008$, partial-$\eta^2 = .172$, $BF_{10} = 6.868$; Figure 2C) probe trials. In both instances, this interaction was driven by significantly greater distance error in the desktop vs. immersive VR condition in older adults (immediate: $t_{(38)} = 2.83$, $p = .007$, $BF_{10} = 3.386$; delayed: $t_{(38)} = 2.96$, $p = .005$, $BF_{10} = 58.497$), along with a null effect of VR condition among young adults (immediate:

$t_{(38)} = -1.18$, $p = .245$, $BF_{10} = 0.478$; delayed: $t_{(38)} = -1.00$, $p = .322$, $BF_{10} = 0.314$). Significant age differences in spatial precision were evident in the desktop VR condition (immediate: $t_{(38)} = 4.12$, $p = 2.0^{-4}$, $BF_{10} = 119.569$; delayed: $t_{(38)} = 3.59$, $p = .001$, $BF_{10} = 33.057$), although the differences did not reach significance in the immersive condition (immediate: $t_{(38)} = 1.87$, $p = .070$, $BF_{10} = 1.195$; delayed: $t_{(38)} = 1.49$, $p = .144$, $BF_{10} = 0.740$). Note that the Bayes factor values computed for the immersive VR condition for old vs. young indicated weak or 'anecdotal' evidence in favor of the alternative (immediate probe) and null (delayed probe) hypotheses.

Interactions between age and VR condition on spatial precision remained significant after controlling for total distance travelled and time spent navigating (see supplemental materials and Supplementary Figures S1 and S2). Taken together, these results suggest that the precision of immediate and delayed spatial recall in older adults was significantly worse when tested in the desktop virtual environment, and this could not be explained by systematic age- or condition-related differences in navigation efficiency. By contrast, spatial performance in young adults was unaffected by the respective VR modalities.

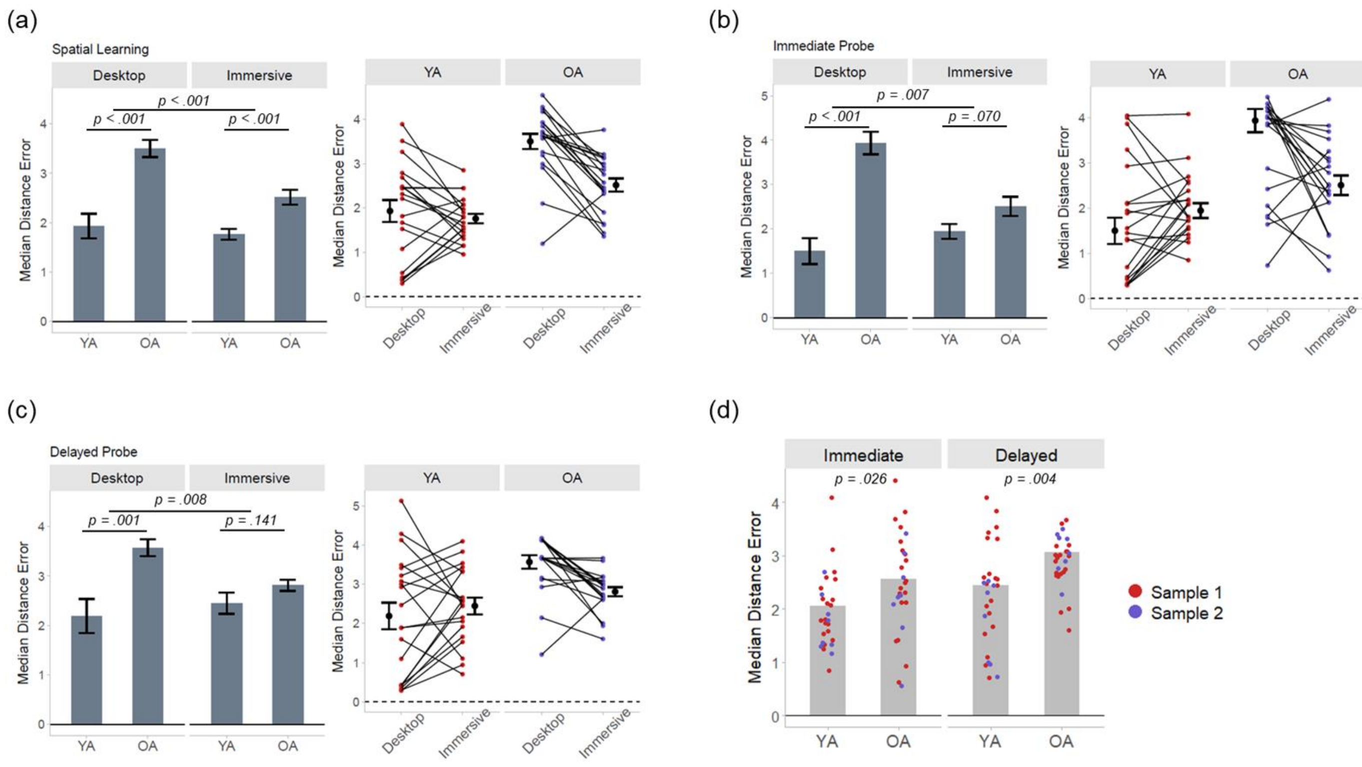

Figure 2. Median spatial distance error is plotted for (a) the spatial learning blocks, (b) immediate probe trials, and (c) delayed probe trials. The spaghetti plots illustrate within-subject changes in distance error between the respective VR conditions. (d) Spatial precision during the immediate and delayed probe trials is plotted for the immersive VR condition with data combined from the original 40 participants (red) and the independent sample of 16 participants (blue). In this expanded sample, spatial precision was reliably worse in older compared to younger individuals during the immediate and delayed probe trials.

Independent validation of age differences in the immersive VR condition

As described in the foregoing paragraphs, post-hoc tests did not reveal a significant age difference in the immersive VR condition on immediate and delayed probe trials, although the Bayes factor indicated that this finding was ambiguous. The lack of a significant age difference in immersive VR was surprising given prior evidence of significant age differences in rodents and humans when navigating 'real space'[19–22], which was functionally akin to our immersive VR condition (see also[18]). As can be seen in the left panels of Figs 2B and 2C, a numerical decrease in distance error was evident in young compared to older adults during these trials. One possibility is that the above analyses lacked sufficient power to detect subtle age-related effects (Cohen's d = 0.59 and 0.47 for the immediate and delayed probe trials, respectively).

To examine this issue further, we recruited an independent sample of 16 participants (8 young, 8 older) to provide greater statistical power to detect effects in the immersive VR condition (note that this cohort of participants did not complete the desktop version of the task). We performed separate two-tailed independent t-tests (equal variances not assumed) on data combined across the initial 40 participants (immersive VR condition only), and the 16 additional participants (N = 28 in each age group). We found a significant effect of age during the immediate ($t_{(49.46)} = 2.30$, $p = .026$, $BF_{10} = 2.309$) and delayed ($t_{(40.53)} = 3.09$, $p = .004$, $BF_{10} = 12.041$) probe trials. These data are illustrated in Figure 2D.

Reduced spatial precision when navigating from novel vs. familiar viewpoints

During the delayed probe trials, participants were cued to recall hidden target locations from familiar start locations (i.e., those encountered during previous spatial learning trials) as well as from novel start locations not previously encountered. Prior studies have employed familiar and novel start locations as assays of egocentric and allocentric navigation, respectively[18,23–25]. Consistent with prior studies, we tested whether older adults showed greater 'switching costs' when taking a novel vs. familiar route to locate the hidden target[26,27].

We submitted median distance error during delayed probe trials to a three-way mixed-factorial ANOVA with factors of age, VR condition, and start position (novel, familiar; Figure 3). The ANOVA gave rise to a significant main effect of start position ($F_{(1,38)} = 32.05$, $p = 1.66^{-6}$, partial-$\eta^2 = .458$, $BF_{10} = 14.346$) which was driven by greater distance error when starting from a novel compared to repeated viewpoint in both age groups ($t_{(38)} = 5.66$, $p < .0001$). The interaction between age and start location was also significant ($F_{(1,38)} = 5.05$, $p = .031$, partial-$\eta^2 = .117$, $BF_{10} = 89.630$). Post-hoc t-tests revealed a greater effect of switching costs in older ($t_{(38)} = 5.59$, $p < .0001$) relative to younger ($t_{(38)} = 2.42$, $p < .021$) adults. The respective two- and three-way interactions involving VR condition were each far from significant ($p > .2$). Our findings suggest that while both groups performed worse at remembering the target from a novel start point, the precision costs of switching between a familiar and novel viewpoint were greater in older relative to younger adults.

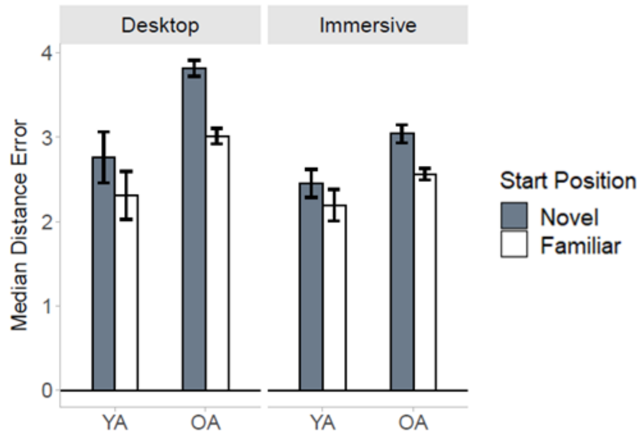

Figure 3. Spatial precision during delayed probe trials is plotted as a function of starting from novel and familiar viewpoints. Distance error was greater when starting from a novel start location. The costs of switching between familiar and novel viewpoints during navigation was twice as large in older compared to younger individuals.

Age differences in reliance on multiple distal cues were not moderated by VR condition

We next examined the subset of probe trials in which a single distal mountain cue was rotated 20º clockwise or counterclockwise. We reasoned that among those participants relying on a single mountain cue to locate the hidden target, distance error would predicably rotate along with the moved mountain. By contrast, participants that triangulated their position using multiple distal mountain cues would be less affected by the single rotated mountain[18]. To this aim, we computed the distance error between a given object's remembered location and the hypothetical location of that object if it were rotated 20º commensurate with the rotated mountain cue (rotated error). We then divided the rotated error by the sum of the rotated error and the true distance error between the estimated and true (unrotated) location of that target object [error index = rotation error / (rotation error + true error)]. Values approaching 0 signify greater weighting of the rotated mountain cue (i.e., beacon strategy), values approaching 1 indicate greater weighting of the three stationary mountain cues (i.e., allocentric strategy), and values of .5 indicate a mixture of strategies.

The rotation indices for each age group and VR condition are illustrated in Figure 4. Young adults were more likely to rely on the three unmoved mountains when locating the hidden target compared to their older counterparts ($F_{(1,37)} = 19.51$, $p = 8.0^{-5}$, partial-$\eta^2 = .345$, $BF_{10} = 30.335$; desktop: $t_{(37)} = -2.97$, $p = .005$, $BF_{10} = 9.380$; immersive: $t_{(37)} = -2.56$, $p = .015$, $BF_{10} = 3.679$). Age differences on the rotated mountain trials were invariant with respect to the two VR conditions, as evidenced by a non-significant age group x VR condition interaction ($F_{(1,37)} = 1.49$, $p = .230$, partial-$\eta^2 = .039$, $BF_{10} = 0.651$). Post-hoc *t*-tests further confirmed that the rotation indices did not reliably differ between the respective VR conditions in young ($t_{(18)} = 1.04$, $p = .310$, $BF_{10} = 0.383$) or older ($t_{(37)} = -0.59$, $p = .558$, $BF_{10} = 0.273$) adults.

To clarify whether young and older adults showed a preference for one strategy over another, we performed one-sample *t*-tests (two-tailed) to compare error indices against a hypothetical mean of 0.50 separately for each age group and VR condition. Error indices were significantly greater than 0.50 among young adults in the desktop ($t_{(19)} = 2.54$, $p = .020$, $BF_{10} = 1.446^9$) and immersive ($t_{(18)} = 2.45$, $p = .025$, $BF_{10} = 8.073$) VR conditions, suggesting a potential greater reliance on allocentric strategies in young adults relative to older individuals. Error indices in older adults did not significantly differ from 0.5 in either of the VR conditions (desktop: $t_{(19)} = -1.79$, $p = .090$, $BF_{10} = 1.167$; immersive: $t_{(19)} = -0.91$, $p = .375$, $BF_{10} = 2.554$). We interpret this to reflect that although both groups used a combination of allocentric and beacon strategies, younger adults employed multiple distal cues to a slightly but significantly greater extent than older adults.

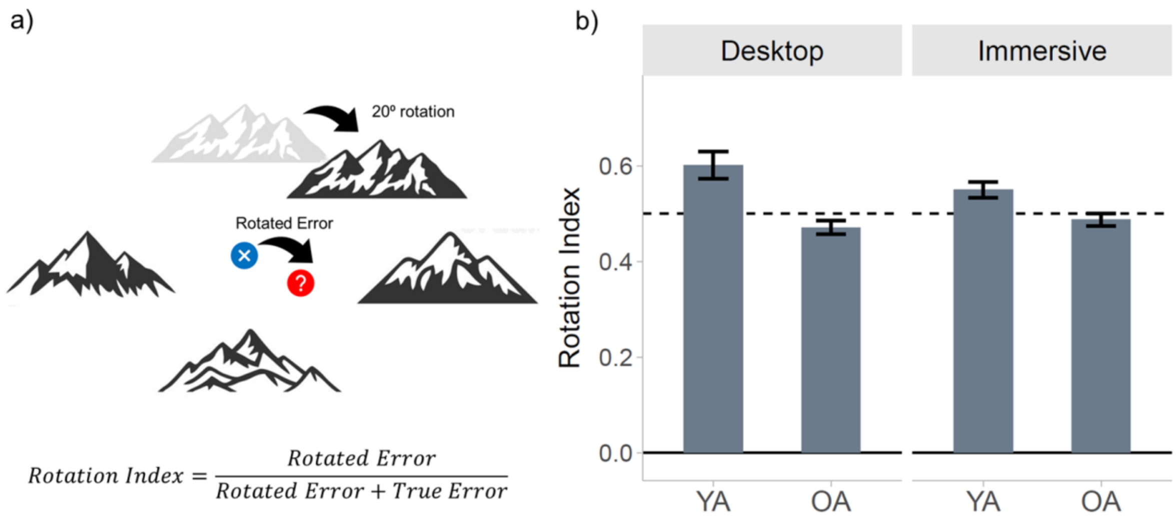

Figure 4. Rotated mountain trials. (a) A singular distal mountain cue was rotated 20 degrees clockwise or counterclockwise on a subset of the delayed probe trials. The blue and red dots indicate the actual and hypothetical rotated location of the hidden target, respectively. (b) A main effect of age was driven by higher rotation indices in young relative to older adults, indicating that younger adults were more likely to locate the hidden target in reference to the three stationary mountain cues.

Both age groups orient towards the hidden target and/or distal mountain cues

In a final set of analyses, we examined whether young and older adults differed in their relative tendency to orient towards the location of a hidden target or the distal mountain cues during the delayed probe trials. To this aim, we performed a Rayleigh's test of uniformity separately for each age group and VR condition using heading orientations recorded at the time a memory response was made. We reasoned that a memory for the target location would result in orientations clustered around the hidden target location and/or distal mountain cues, whereas a failure to triangulate the correct target location would result in a uniform distribution of heading orientations.

Group-level Rayleigh's tests confirmed that heading orientations at the time of retrieval were not uniformly distributed for either of the VR conditions in younger (*ps* $< .001$) or older (*ps* $\leq .03$) adults. Polar histograms were created to qualitatively illustrate the frequency of heading directions at the time a memory response was recorded (Figure 5). These plots suggest that both young and older adults generally oriented towards the correct location of the hidden target objects (solid red lines) or the distal mountain cues (dotted blue lines) regardless of the VR condition. These findings suggest that older adults oriented and employed distal cues in a similar manner to younger adults, although when faced with an option of a moved mountain, tended to weight this more strongly than the collection of distal cues.

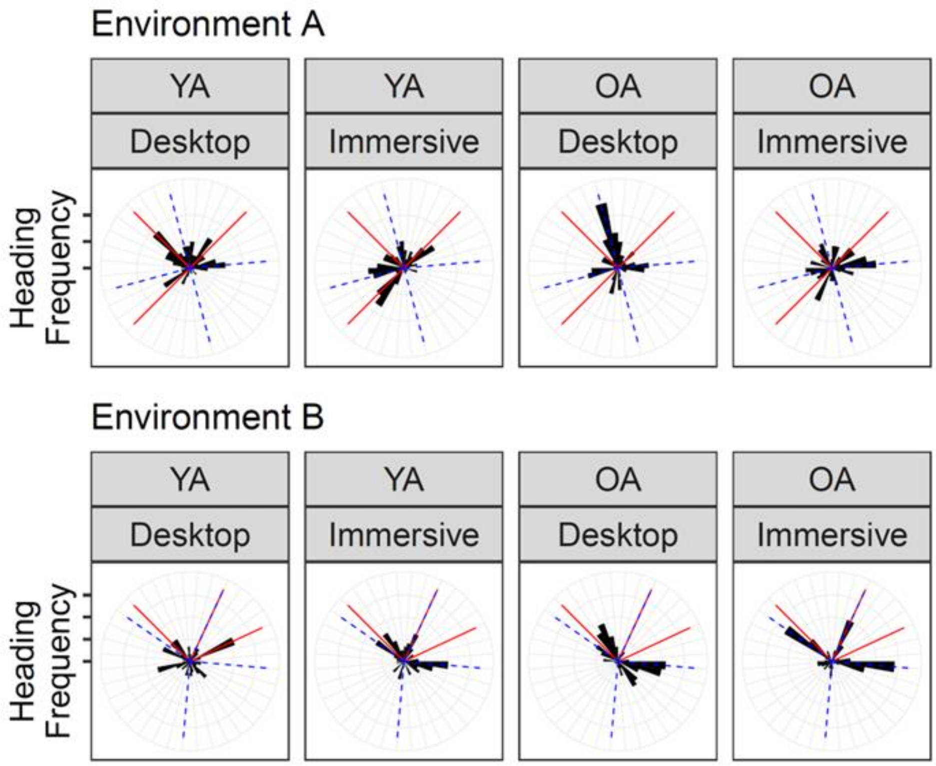

Figure 5. Frequency of heading orientations at the time a memory response was made during delayed probe trials. Plotted separately for each age group, VR condition, and environment. Solid red lines correspond to the heading orientation of the hidden target location. Dashed blue lines correspond to the heading orientation of the four distal mountain cues.

Discussion

Traditional models of human aging and navigation are largely predicated on findings from experimental paradigms employing desktop-based VR to assay spatial abilities. We used a virtual Morris Water Maze (vMWM) paradigm and observed robust evidence that age-related differences in the precision of spatial memories were moderated by the modality of the virtual testing environment. Reliable age differences in immediate and delayed spatial recall were evident in a virtual desktop condition that required using a keyboard and mouse to navigate, replicating numerous prior studies[1,5,28]. The size of these age differences were attenuated, however, when tested in an immersive virtual condition that permitted free ambulation during navigation. These effects were driven by disproportionately worse performance in older adults when navigating a virtual desktop environment, which restricted self-generated idiothetic feedback and was potentially less familiar and natural to the older cohort. These findings are consistent with prior observations that age differences in path integration are reduced or even eliminated when multisensory cues are available during navigation[15,16]. We emphasize, however, that the vMWM task evokes spatial computations that are inherently distinct from those involved with successful path integration, most critically, the need to integrate distal visual landmarks with idiothetic-driven path integration computations[29–31]. Our findings thus provide new insights into the nature of age differences in spatial memory by suggesting that at least one factor driving the extent of these differences relates to the testing modality.

In marked contrast to the older adults, spatial precision in young adults did not reliably differ between the two testing modalities. This finding converges with reports from prior studies that compared spatial performance in young adults while navigating desktop-based and immersive ambulatory VR environments. A common finding from these studies is that young adults show little differences in spatial performance when provided with sufficient learning[32,33] and can transfer significant amounts of knowledge from a desktop virtual environment to a real-world one[12,13]. Younger adults may therefore benefit from prior computer gaming and VR experience. Consistent with this, our findings suggest that younger adults may be able to learn from desktop VR as effectively as immersive VR, particularly in a paradigm such as the vMWM involving extensive learning and exposure to the environment.

Spatial navigation is an inherently complex construct that draws on multiple sensory systems (e.g., visual, proprioceptive, vestibular, and motoric), each of which is susceptible to advancing age[34–37]. Our findings suggest that age differences in the precision of spatial memories are significantly reduced in an immersive virtual environment in which visual and self-motion cues are available to guide navigation. One possibility is that older adults place a greater reliance on complementary sensory cues to compensate for reduced acuity in other sensory domains. Consequently, the lack of body-based cues in the desktop environment, which favored primarily visual input, may have affected older adults' ability to encode spatial representations in sufficient detail to support accurate spatial memory[38]. Though this account is speculative, it is consistent with prior reports that age differences in navigation performance arise, at least in part, from a failure to combine information from different sensory modalities, resulting in noisier spatial representations[39–41].

Younger adults were more likely than their older counterparts to triangulate the location of the hidden target in reference to the three unmoved mountains rather than using the single moved mountain. Findings from the viewpoint analysis (familiar vs. novel start) further suggested that older adults performed worse at remembering the target location from a new start point rather than a repeated one. Critically, these age differences were seemingly invariant with respect to VR condition. Taken together, these findings suggest that older adults may be biased towards navigating with reference to a familiar viewpoint and/or single distal cue, which would be consistent with past work suggesting a bias toward response learning in older adults[26,28]. It is worth noting that neither the viewpoint nor the rotated mountain analyses reported here provide a process pure measure of allocentric vs. egocentric navigation strategies[42]. By some accounts, navigation errors in older age are considered to stem, at least in part, from a failure to switch between navigation strategies[5,26,27]. Another possibility is that older adults fixate on distal landmarks less effectively than younger individuals due to perceptual processing deficits, but maintain the ability to engage in allocentric navigation strategies when additional spatial cues are available, such as geometry-based cues[43]. As such, inefficient switching between different strategies according to available cues and task demands may account for much of the age-related variance often observed in navigational abilities.

In a recent study from our laboratory using a similar version of the vMWM task in immersive VR (but not desktop VR)[18], we found that older adults remembered target locations with lower spatial precision than younger adults. We replicated the same basic finding in the current study, suggesting that older adults show some reduced precision even in immersive VR. Together, these findings suggest that, even under more naturalistic settings, some age-related differences in spatial precision persist. In the McAvan et al. study, however, we also found that young and older adults did not differ when switching from familiar to novel viewpoints, nor did the two age groups reliably differ in their tendency to prefer a beacon strategy on rotated mountain trials. An important difference in our paradigms is that McAvan et al. provided continuous feedback during both learning and probe trials by showing the correct location of the hidden object following a memory response. In the present study, such feedback was only available during learning trials. Thus, it is possible that this discrepancy between our results stemmed from the availability of this feedback during probe trials.

In the foregoing discussion, we suggest that impaired spatial memory observed in older adults navigating a desktop environment stem from a lack of self-generated idiothetic feedback and/or a combination of age-related confounds such as limited exposure to computer gaming equipment or reduced visual and sensorimotor acuity. Although these possibilities are certainly not mutually exclusive, the present data do not allow us to adjudicate between the factors that drove spatial memory deficits in the desktop VR environment. Another limitation of the present study concerns the ecological validity of the sparse environment encountered in the vMWM task. Prior work has shown that age differences in navigation performance are attenuated when navigating in highly familiar environments, such as a local supermarket[22]. Future research is needed to address whether the moderating effect of VR modality extends to familiar and/or hyper-realistic environments that more closely approximate the types of scenes and challenges older adults face in their daily lives.

In conclusion, marked age differences in the precision of spatial memories were evident when using a keyboard and mouse to navigate a virtual desktop MWM environment. These age differences were reduced, however, when navigating in a fully immersive and ambulatory vMWM environment that permitted unrestricted locomotion and idiothetic feedback. Taken together, these results suggest that the lack of self-generated feedback when navigating a virtual desktop environment affected the fidelity of spatial representations in older adults which could not be wholly accounted for by a failure to engage in allocentric search strategies.

Materials and Methods

Participants

We recruited 21 young and 22 older adults from the University of Arizona and surrounding communities. One older adult voluntarily withdrew from the study due to a scheduling conflict; one young and one older adult withdrew after experiencing mild motion sickness during the virtual reality task. The final participant sample included 20 young adults (18-27 yrs.; M = 21.15 yrs; SD = 2.30 yrs; 12 females) and 20 older adults (66-80 yrs.; M = 73.30 yrs.; SD = 3.89 yrs.; 7 females). We also recruited an independent sample of 8 young (19-24 yrs; M = 21 yrs; SD = 2 yrs; 6 females) and 8 older (67-80 yrs; M = 71.25 yrs; SD = 5.23 yrs; 5 females) to complete the immersive VR condition of the task. This independent cohort was recruited in an effort to detect what the Bayes factor analysis suggested could be an underpowered age-related difference when navigating during unrestricted locomotion. Note that this sample of participants did not perform the desktop VR task. All participants gave informed consent in accordance with the University of Arizona Institutional Review Boards and were compensated at the rate of $18 per hour. All participants had normal or corrected-to normal color vision, normal or corrected-to-normal hearing, and reported no history of cardiovascular problems, neurological conditions, or history of motion sickness.

Neuropsychological Test Battery

All older adult participants completed a neuropsychological test battery on a day prior to the experimental MRI session. The test battery included multiple tests and scores in each of four broad cognitive domains: memory [California Verbal Learning Test-II (CVLT) Long Delay Free Recall[44], Rey-Osterrieth Complex Figure Test Long Delay Free Recall (RCFT-LDFR)[45]], executive function [Trail Making Tests A and B total time][46], language [F-A-S fluency[47], category fluency[48], Boston Naming Test (BNT); Goodglass et al., 2001], visuo-spatial abilities [Wechsler Adult Intelligence Scale 4th edition (WAIS-IV) Block Design test[49], RCFT copy score[45]], and verbal intelligence [WAIS-IV Vocabulary and Similarities][49]. Participants were excluded from entry into the study if they scored < 1.5 SDs below age-appropriate norms on any memory test or < 1.5 SDs below age norms on any two other tests. These criteria were employed to minimize the likelihood of including older individuals with mild cognitive impairment, individuals who are considered at elevated risk for Alzheimer's disease and related dementias. Results from the neuropsychological test battery are presented in Supplementary Table S1.

Virtual Environments

The virtual environment and experimental tasks were built in Unity 3D (Unity Technologies ApS, San Francisco, CA) using the Landmarks virtual reality navigation package[50]. The navigable virtual environment was approximately 5x5 m in size, with the full space spanning 750x750 m. Four distally rendered mountains were visible from within the 5x5 m space. Each virtual environment was rendered with a unique floor (snow-covered or desert), and three unique 3D rendered objects (book, puzzle cube, teapot in the snow-covered environment; alarm clock, mug, rotary phone in the desert environment). These objects were presented on pedestals at approximately chest height and served as the hidden navigation goals (see Procedures). The respective virtual environments and order of administration were fully counterbalanced across the immersive and desktop VR conditions.

Immersive VR Condition. To simulate the immersive experience of being in a mountainous environment, we used the HTC Vive Pro headmounted display (HMD) in conjunction with the HTC wireless Adapter (HTC, New Taipei City, Taiwan) to allow for untethered, free ambulation. The Vive Pro displayed stimuli at a resolution of 1140-1600 pixels per eye, 90 Hz refresh rate, and a 110º field of view, while the Wireless Adapter delivered data over a 60 GHz radio frequency for up to 7m. Participants were allowed to interact with the virtual environment and record their responses using a handheld HTC Vive controller (HTC, New Taipei City, Taiwan). The immersive VR task was run on a custom-build computer with a NVIDIA GeForce Titan Xp graphics card (NVIDIA Corp., Santa Clara, CA, United States.

Desktop VR Condition. All participants navigated an analogous version of the MWM task optimized for a laptop computer. The desktop VR condition was completed in a quiet behavioral testing room with participants seated approximately 2' from the screen. The task was run on a 15" Lenovo Legion Y540 gaming laptop computer with a GTX1660 Ti graphics card. Forward, left, backwards, and right translations were made by pressing the 'W', 'A', 'S', and 'D' keys, respectively. Participants could simultaneously use the mouse to rotate their view around the xyz axis.

Navigation Procedures

Prior to beginning the immersive phase of the experiment, participants were instructed to close their eyes as they were led into the navigation room. This prevented participants from seeing the size and shape of the physical environment and heightened the level of immersiveness. Upon entering the navigation room, participants were fitted with the wireless HMD, a handheld controller (held in their dominant hand), and a clip-on battery pack that powered the wireless HMD. Participants were then immersed in a practice virtual environment similar to the main task described here. During the practice phase, participants were allowed to freely navigate a small circular room for five trials lasting 30 seconds before being prompted to find and remember the location of a single target object for a subsequent five trials. The practice session lasted approximately 10 min. Participants completed an identical practice session prior to beginning the desktop condition to ensure proficiency with using the keyboard and mouse to navigate.

After the practice session in each VR condition, participants were tasked with completing five blocks of a navigation task. Participants were offered an opportunity to take brief breaks in-between each block. The study design was based on a prior study conducted in healthy young and older adults performed in an immersive VR environment[18]. A similar version of this task was also used with amnestic patients in a desktop VR environment[24]. In each task block, participants received verbal and visual instructions and were provided with reminders when requested. White noise was played through headphones throughout the experiment to prevent sound cues from providing location or orientation information.

After completion of each trial, participants were briefly disoriented by guiding them around the environment without vision. This prevented participants from tracking their bearing and movements through the environment from trial to trial and thus ensuring participants used their memory to find the target locations. During the immersive VR condition, participants were physically guided by a research assistant along a random path while the HMD presented a blank screen. During the desktop VR condition, participants viewed a blank screen during the disorientation period, after which they were placed in the next start location. The order and sequence of the start locations were held constant for each virtual environment across all participants.

Spatial Learning Block. Participants were familiarized with the locations of the six target objects (three in each VR environment) by performing 16 blocked spatial learning trials. Before each trial, participants were disoriented for 30 s and then placed at one of eight starting positions. Each spatial learning block was organized into four sub-blocks, each corresponding to a unique start position (e.g., 4 consecutive trials from position 1, followed by 4 consecutive trials from position 5, etc.). Each trial began with visual instructions indicating the navigation goal (e.g., 'Please find the book'). Participants then freely navigated the environment until the target object appeared after 30 s.

After the first trial of each learning block, participants were encouraged to remember the location of the target object and to walk to that location before 30 s elapsed. Participants had the option to make a button response if they were confident they had navigated to the correct target location. This was recorded as a spatial memory response and the location and timestamp of this response were logged in the data output. Upon making a button press, the target object became visible and participants were instructed to touch the object with the handheld controller to move to the next trial. If a button response was not made, the target object would appear after 30 s, at which point the location and timestamp were logged in the data output and participants were permitted to touch the object to move to the next trial.

Immediate Spatial Probe Trials. After 16 trials of each spatial learning block, participants performed a single probe trial. Participants were placed in a novel start position and tasked with recalling the location of the target object. Participants were instructed that the object would not appear after 30 s, nor would the object appear after making a button press. Note that this differed from McAvan et al.[18] in which the object appeared immediately after the button press. The trial commenced with visual instructions indicating the navigation goal (e.g., 'Please find the book'). Upon reaching the location of the hidden target object, participants made a button press and their location and timestamp was logged in the data output. Participants then had the opportunity to take a brief break before moving onto the next block.

Visual Target Block. Following the three spatial learning blocks, participants completed one block of eight visible target trials. The target objects remained visible for the entire duration of these trials. As discussed in the introduction, these trials served as a control for motivational and potential sensorimotor deficits in performing the task[6,51], although they have also been employed as a comparison for "egocentric" navigation. Before each trial, participants were disoriented for 20 s while the virtual environment was blacked out. Each trial began with visual instructions indicating the navigation goal (e.g., 'Please find the book'), at which point the participants simply walked to the visible object and touched it with the handheld controller in order to progress to the next trial. Each target object was presented in sequential order (i.e., target 1, target 2, target 3, target 1, target 2, etc.).

Delayed Spatial Probe Trials. Following the visible target block, participants performed 12 probe trials designed to test delayed spatial recall. Before each trial, participants were disoriented for 20 s while the virtual environment was blacked out. Each trial began with visual instructions indicating the navigation goal (e.g., 'Please find the book'). Participants were instructed to find each target object in sequential order (e.g., target 1, target 2, target 3, target 1, target 2, etc.). Six of the 12 delayed probe trials began from a start position that previously accompanied that target object during the spatial learning block ('repeated' trials). The remaining six delayed probe trials began from a novel start position that was not previously linked to the target object ('novel' trials). As with the immediate probe trials, the target object did not appear after 30 s, nor did it appear after a button press. Again, this differed from McAvan et al.[18] in which the object appeared immediately after the button press. Participants were thus required to navigate to the location of the hidden target object based solely on their memory. Upon reaching this location, participants made a button press to record their location and timestamp.

Rotated Mountain Trials. The final block comprised three probe trials that were similar to the immediately preceding delayed probe trials, the sole difference being that one of the distal mountain cues was rotated 20º clockwise or counter clockwise around the target. The objective was to explore how manipulation of the distal navigation cues affected spatial memory accuracy. If participants used a single mountain cue to navigate (i.e., a beacon strategy), their spatial memory should be similarly rotated by 20º in the same direction. Alternatively, if participants triangulated the position of the hidden target object using multiple mountain cues to derive an allocentric coordinate, their memory should be largely unaffected by the moved mountain cue.

Statistical Analyses

Position and rotation data was recorded throughout the entire experiment at a sampling rate of approximately 10 Hz. All statistical analyses were conducted with R software (R Core Team, 2017). All *t*-tests were two-tailed and performed using the t.test function in the base R package. Welch's unequal variance *t*-tests were performed when assumptions of equal variance were not met. ANOVAs were conducted using the *afex* package[52] and the Greenhouse-Geisser procedure[53] was used to correct degrees of freedom for non-sphericity when necessary. Post-hoc tests on significant effects from the ANOVAs were conducted using the *emmeans* package[54] and corrected for multiple comparisons using the Holm-Bonferroni procedure where appropriate. Bayes factor values were computed using the *BayesFactor* package[55].

Spatial precision was operationalized as the Euclidean distance between the remembered and true location of each target object (i.e., distance error). We computed the median trial-wise distance error separately for each participant and experimental block [Spatial Learning, Spatial Probes (Immediate and Delayed), Rotated Mountains]. During the spatial learning block, the *remembered* location corresponded to a participant's location when a memory response was indicated on the handheld controller/mouse or, in the absence of an overt button response, by recording participant location after 30 seconds had elapsed and the target object became visible. During the immediate recall, delayed recall, and rotated mountains blocks, the *remembered* location always corresponded to the participant location when a memory response was indicated (as the target objects did not appear after any amount of time).

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Supplemental Materials

Table S1. Mean (with SD) z-score performance on the neuropsychological tests for older adults

Test	Mean (SD) z-score
Memory	
CVLT-LDFR	0.39 (1.11)
RCFT LDFR	-0.28 (0.84)
Language	
BNT	0.63 (0.98)
F-A-S Fluency	0.48 (1.27)
Animal Fluency	0.51 (1.30)
Executive Function	
Trails A	-0.37 (0.73)
Trails B	0.13 (0.88)
Digit Span	0.62 (0.94)
Visuospatial Function	
WAIS Block Design	0.76 (0.88)
Matrix Reasoning	1.47 (0.82)
RCFT Copy	-0.74 (0.76)
Verbal Intelligence	
WAIS Vocabulary	1.33 (0.65)
WAIS Similarities	1.13 (0.62)

CVLT, California Verbal Learning Test; RCFT, Rey-Osterrieth Complex Figure Test; LDFR, Long Delay Free Recall; BNT, Boston Naming Test; WAIS, Wechsler Adult Intelligence Scale

Speed-accuracy tradeoff is not moderated by age or VR condition

We next examined the effect of age group and VR condition on the amount of time spent navigating during the delayed probe trials, as older adults could be compromising reaction time for accuracy (Salthouse, 1991). For each trial, we computed the log-transformed latency between trial onset and the button response marking spatial memory. We then computed the median trial-wise navigation latency and submitted these values to a two-way mixed-factorial ANOVA with factors of age group and VR condition. This analysis revealed a significant main effect of age group ($F_{(1,38)}$ = 9.04, p = .005, partial-η^2 = .192) which was driven by *shorter* navigation latencies in older relative to younger adults ($t_{(38)}$ = -3.01, p = .005), and a significant main effect of VR condition ($F_{(1,38)}$ = 11.91, p = .001, partial-η^2 = .239) which was driven by shorter navigation latencies in the desktop relative to immersive VR condition ($t_{(38)}$ = -3.45, p = .001). The interaction between age group and VR condition was not significant ($F_{(1,38)}$ = 0.04, p = .838, partial-η^2 = .001).

The amount of time spent navigating during the delayed probe trials negatively covaried with distance error (r = -.40, p = 2.0^{-4}). We performed a multiple regression analysis to determine whether this speed-accuracy tradeoff was moderated by age group and/or VR condition. Median distance error was entered as the dependent variable, and log-transformed navigation time, age group, VR condition, and all first-order interaction terms involving navigation time were entered as predictor variables. The main effect of navigation time on distance error remained significant when controlling for age group and VR condition ($r_{partial}$ = -.28, p = .011). The time x age and time x condition interactions terms were each far from significant (ps > .3). These analyses confirm that neither age group nor VR condition reliably moderated the negative relationship between distance error and navigation speed.

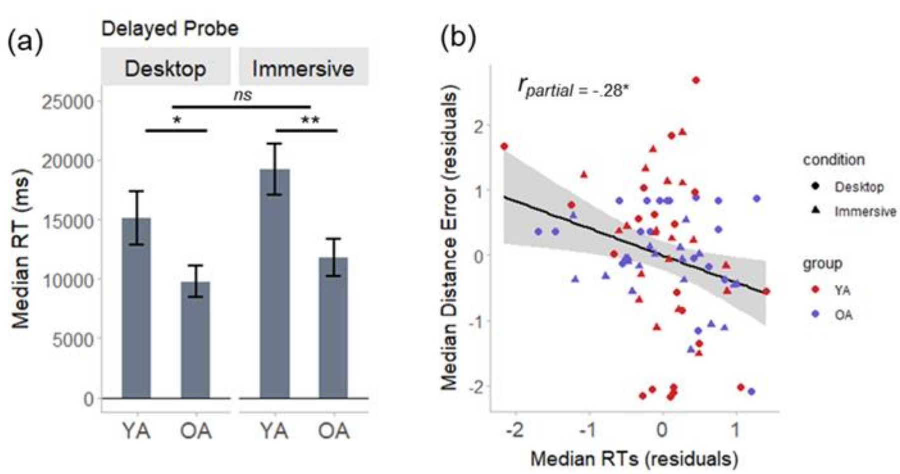

Figure S1. (a) Response latencies during the delayed probe trials were greater in younger relative to older adults, and for the immersive relative to the desktop condition. Age differences in response latencies were not moderated by VR condition. (b) Response latencies during the delayed probe trials negatively covaried with distance error. This speed-accuracy tradeoff was not moderated by age group or VR condition. *p < .05, **p < .01, ***p < .001.

Age differences in total distance travelled in the delayed probe trials are moderated by VR condition but do not fully account for commensurate age differences in spatial precision.

We computed the total distance travelled on each delayed probe trial and submitted the median value to a two-way mixed-factorial ANOVA with factors of age and VR condition. Though age differences were highly significant in both the desktop and immersive conditions ($t_{(38)} = -4.80$, $p < .001$; $t_{(38)} = -4.11$, $p < .001$, respectively), a significant interaction ($F_{(1,38)} = 6.31$, $p = .016$, partial-$\eta^2 = .142$) between age and VR condition confirmed that age differences in total distance traveled were reliably greater in the desktop condition. Motivated by these findings, we regressed out the effects of total distance on distance error and then submitted the resultant residualized distance error values to a two-way ANOVA with factors of age group. and VR condition. The interaction between age group and VR condition on distance error remained significant when controlling for total distance travelled ($F_{(1,38)} = 5.88$, $p = .020$, partial-$\eta^2 = .134$).

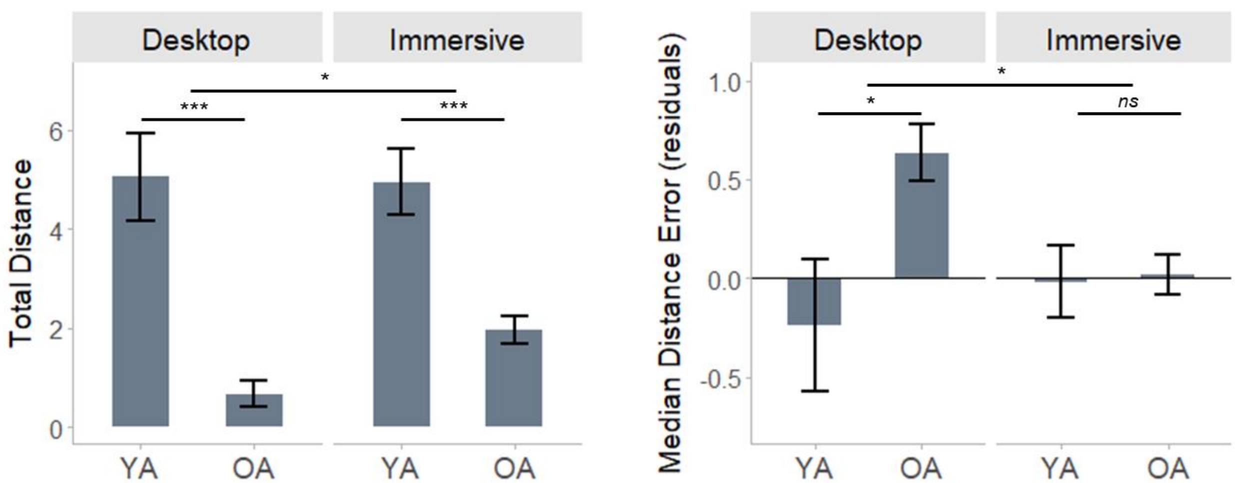

Figure S2. Total distance travelled on the delayed probe trials plotted by age group and VR condition (left panel). Traveled distances were greater in younger relative to older adults, and in the immersive relative to desktop condition. A significant age x condition interaction confirmed that the age-related effect size was reliably greater in the desktop VR condition. The interaction between age and VR condition on medial distance error (i.e., spatial precision) during the delayed probe trials remained significant after controlling for age- and condition-related differences in total distance travelled. *$p < .05$, **$p < .01$, ***$p < .001$, *ns* = not significant.

VR condition, but not age, moderates navigation performance during visible target trials

Following the three spatial learning blocks, participants completed one block of eight visible target trials, during which the targets remained visible for the duration of the trial. These trials were included to rule out potential age-related motivational and/or sensorimotor deficits which may have confounded performance on the task. A 2 (age group) x 2 (VR condition) ANOVA of distance error revealed a significant main effect of condition ($F_{(1,38)}$ = 11.29, p = .002, partial-η^2 = .229) which was driven by greater distance error in the immersive (M = 1.13, SD = .21) relative to the desktop (M = 0.90, SD = .27) VR condition. The main effect of age and the age x condition interaction were not significant (ps > .1).

For each participant, we computed the median log-transformed time it took to reach the visible targets and submitted these values to a 2 (age group) x 2 (VR condition) ANOVA. The analysis revealed a main effect of VR condition ($F_{(1,38)}$ = 3.98, p = .053, partial-η^2 = .095) which was slightly beyond the *a priori* significance criterion (α < .05). This marginal effect was driven by shorter navigation times in the immersive (M = 6972 ms, SD = 3546 ms) relative to the desktop (M = 9421 ms, SD = 9161) VR condition. The main effect of age and the age x condition interaction were not significant (ps > .1)

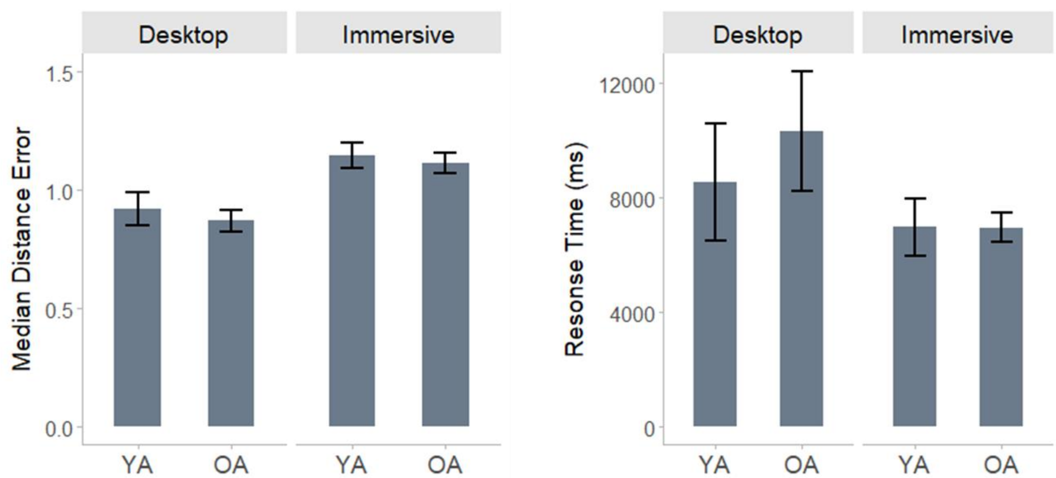

Figure S3. Significant main effects of distance error (left panel) and navigation response time (right panel) were evident during the visible target trials. Neither the main effect of age nor the interaction between age and VR condition were significant.