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Age differences in spatial memory in a virtual environment navigation task

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Abstract

The use of virtual environment (VE) technology to assess spatial navigation in humans has become increasingly common and provides an opportunity to quantify age-related deficits in human spatial navigation and promote a comparative approach to the neuroscience of cognitive aging. The purpose of the present study was to assess age differences in navigational behavior in a VE and to examine the relationship between this navigational measure and other more traditional measures of cognitive aging. Following pre-training, participants were confronted with a VE spatial learning task and completed a battery of cognitive tests. The VE consisted of a richly textured series of interconnected hallways, some leading to dead ends and others leading to a designated goal location in the environment. Compared to younger participants, older volunteers took longer to solve each trial, traversed a longer distance, and made significantly more spatial memory errors. After 5 learning trials, 86% of young and 24% of elderly volunteers were able to locate the goal without error. Performance on the VE navigation task was positively correlated with measures of mental rotation and verbal and visual memory. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Navigation; Hippocampus; Age; Spatial memory; Route learning; Virtual reality; Maze; Human

1. Introduction

Age-related deficits in spatial maze-learning are evident in both place and route learning tasks in a number of mammalian species [5,23,35]. In the rodent hippocampus, “place cells” which respond to particular locations in space [29] change their response characteristics with age. It is thought that these and other cellular alterations in the hippocampus and other cerebral structures may underlie the age-related behavioral deficits observed in spatial learning tasks in non-human species [6,7,51,56].

There have been few studies that have systematically examined age-related vulnerability in route-learning or topographical memory in humans. Survey research indicates that elderly individuals have self-perceived deficits in navigation and develop behavioral patterns to avoid unfamiliar routes and places [10]. Direct assessments of navigational/route finding skills in non-demented elderly adults provide evidence of age-related differences in these skills [26,27,41,61]. Furthermore, clinically relevant impairments in navigational skills are often apparent in the early stages of dementia [28,46], in many cases contributing to the diagnosis [3,37]. These results suggest that elderly adults encounter more difficulty than younger adults in learning and remembering routes through novel environments.

The ecological evaluation of route-learning in humans is complicated by the fact that human navigation takes place over relatively large-scale space. It is difficult to gain sufficient control over the external environment to allow the systematic evaluation of human navigation in a controlled setting. The development of virtual environment (VE) technology has made possible a systematic and laboratory-based investigation of navigation in humans [31,58]. These computer-based programs allow simulated exploration of 3D environments from a viewer-centered perspective and allow the experimenter to gain control over environmental stimuli and complexity of the learning environment. Moreover, detailed records of the behavior of individuals within the environment may be recorded and subjected to objective scoring criteria. VE technology has been used successfully in younger participants to assess acquisition of spatial knowledge [20], sex differences in both overall perfor-

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mance [4,36] and strategic use of environmental cues [50], theta oscillations in electroencephalography [25] and regional brain activation patterns in neuroimaging studies [1,21,30,32].

Despite the fact that navigating successfully through the world is clearly an ecologically important aspect of human behavior, the vast majority of studies of human cognitive aging have assessed memory using tests that require the encoding and retrieval of words or geometric figures. In contrast, spatial memory in non-human species is typically assessed using maze learning tasks that require the animal to navigate and remember routes or specific locations in novel environments. Researchers examining behavior in non-human species, particularly rodents, theorize that the hippocampus and related structures may generate representations of the position of an animal in space and continually update this position via the firing of networks of cells responsive to spatial location [15,45], head direction [11], optic flow [63] and other spatial and movement sensitive parameters. These data have led to models which are navigational in nature, or which focus primarily on spatial memory, and emphasize the role of the hippocampus, subiculum and parahippocampal regions. Models of human cognitive aging have been derived primarily from the perspective of episodic memory in which an explicit memory system may be involved in the encoding and explicit recall of events or episodes [12,43]. Although there appears to be considerable divergence between spatial navigation and episodic memory approaches, it seems likely that there is considerable functional, anatomic and evolutionary continuity between these systems [15,38,40,52,54].

The tendency to emphasize different components of cognitive aging and of hippocampal and parahippocampal memory function in particular can be seen to arise primarily from the different behavioral tasks used across species. To investigate cognitive aging from a comparative approach, it is desirable to assess the behavior of human and non-human species under similar behavioral conditions and to develop an understanding of the degree of behavioral and ultimately the neurological overlap between navigational measures of human learning and memory and more traditional cognitive measures.

The purpose of this study was two-fold. Firstly, we quantified the magnitude of age-related decline in VE navigation in a variety of aspects of performance. Secondly, we sought to examine the intercorrelation between our VE navigation task and more traditional psychometric measures of cognitive aging. Because researchers draw similar inferences for cognitive aging from spatial navigational tasks in non-human species and from psychometric measures in humans, it is important to understand the behavioral overlap between these apparently divergent cognitive tasks.

Table 1
Sex and age distribution of sample

	Young (<45 Years)	Middle (45–65 Years)	Old (>65 Years)
Male	14	21	33
Female	14	22	13
Total	28	43	46

2. Methods

2.1. Participants

The sample included 133 individuals—123 participants from the Baltimore Longitudinal Study of Aging (BLSA) and 10 volunteers recruited from Johns Hopkins Bayview Medical Campus. BLSA participants are generally healthy, community dwelling, volunteers who return regularly to the National Institute on Aging for comprehensive medical, physiological and neuropsychological evaluations [53]. Participants meeting NINCDS-ADRDA diagnostic criteria for dementia [34] were excluded from participation. Mean age of the BLSA participants was 57.8 (±18.5) years (range 22–91 years). BLSA participants are generally well-educated, and our sample had a mean education of 16.89 (±2.58) years. Because the age distribution in the BLSA is skewed toward older participants, additional young participants were recruited from the Johns Hopkins Bayview Medical Campus ($N = 10$). These volunteers ranged in age from 20–36 years and were matched to BLSA participants in years of education (16.00 ± 1.70 years). Thirteen participants withdrew from the study due to nausea or dizziness induced by VE exposure (10 women, 3 men, mean age = 76.3 years). The sex and age distribution of the final sample is presented in Table 1. All participants provided informed consent for participation in this study, which was approved by the local institutional review board.

2.2. Procedures

2.2.1. Assessment of level of computer experience

Because elderly participants may have less experience using computers than younger volunteers, all participants completed a computer experience questionnaire prior to VE testing. This questionnaire asked participants to rate the amount of experience they had using a computer, playing computer games, and playing computer games that involve VE technology (e.g. flight or driving simulators). The total score of these 3 items (each rated from 0 to 7) was calculated to obtain an overall computer experience rating for each participant (maximum score = 21).

2.2.2. Pre-test training and assessment of joystick visuomotor control

Prior to maze testing, extensive pre-training was provided to familiarize participants with the VE and with the use of a joystick for movement. This was accomplished with an initial period of experimenter instruction, followed by a period of free exploration of a VE using the joystick. After participants felt comfortable with the joystick and had satisfactorily demonstrated their ability to guide themselves to targets designated by the experimenter, the participants underwent a joystick control speed test. During the speed test, participants were required to navigate a long winding corridor as quickly and accurately as possible until they reached a trophy at the goal point. There were no choice points in the corridor. Prior to administration of the route learning task, participants were required to demonstrate their competency with the joystick by completing the corridor in less than 120 s. Three participants (2 men, 1 woman; mean age = 85 years) were excluded because they had considerable difficulty acquiring the visuomotor skill to use the joystick and could not reach the criterion. Completion time on the joystick control speed test was also incorporated into our statistical analyses as a measure of visuomotor speed to control for residual age differences in visuomotor control of the joystick and general age-related declines in visuomotor processing.

2.2.3. Virtual practice maze

Following the joystick control speed test, a practice maze was presented to participants. The practice maze was similar to the test maze, with the exception that it was of simpler design. Participants were given 3 practice trials on this maze.

2.2.4. Virtual maze learning task

The maze learning task was designed using a modified version of the Game Creation System (Pie in the Sky Software, Fairport, New York, 15334). The task was administered on a Dell IBM compatible Pentium III computer, with a 17“ monitor. The participant viewed a standard computer monitor while seated in a chair. Participants' heads were not restrained but the placement of the chair was such that their head was approximately 50 cm from the computer monitor. The maze was presented from a first person perspective and consisted of a richly textured series of interconnected hallways and alleys. Some hallways of the maze ultimately led to the goal point (designated by a trophy) and others led to dead ends. Landmarks in the form of unique wall textures or objects were located at choice points in the maze. Pilot testing established that a 4 intersection maze with 3 directional choices at each intersection was sufficiently challenging for elderly participants. Participants completed 5 consecutive trials of the same virtual maze and were told to try to locate the goal point as quickly and as accurately as possible and to try to remember the route to the goal over consecutive trials. Movement through the VE was controlled with a Microsoft Sidewinder Precision Pro joystick.

Scoring of the maze learning task was fully automated. A program developed for this purpose recorded the coordinate position of the participant and the heading bearing in degrees every 20 ms. From this record, the time in seconds to complete each trial and the total distance traveled, measured in virtual units, were automatically calculated. In addition, a detailed error analysis was computed. Any deviation from the correct route into a dead end corridor was classified as an error. However, on the first trial, participants had no prior knowledge of the environment to determine which corridors led to the goal and which led to dead ends. Therefore, on the first trial, the first time a participant encountered a dead end, an “information error” was tabulated. On the other hand, repeat visits on the first trial to previously visited error locations were classified as “spatial memory errors.” On the second and all subsequent trials, all errors were classified as spatial memory errors. A spatial memory error was also tabulated when a participant traveled on a portion of the correct route through which they had already traveled, effectively backtracking on their path.

2.2.5. Other cognitive tests

Performance on the VE maze task was examined in relation to other cognitive data available for these participants. Cognitive measures were available for most participants in the BLSA, but cognitive tests were not administered to participants recruited from the Johns Hopkins Bayview Medical Campus. In addition, concurrent cognitive test data were missing for some BLSA participants, because the battery is administered at each visit for participants age 50 and older. Individuals less than 50 years of age receive a single assessment, typically at their initial BLSA visit.

The tests examined in the present study included those for which information was available for the majority of subjects. They included: the Primary Mental Abilities Vocabulary Test ($N = 82$) [13], the California Verbal Learning Test ($N = 75$) [14], the Benton Visual Retention Test ($N = 84$) [8], the Card Rotations Test ($N = 83$) [16], Digit Span Forward and Backward ($N = 83$) and the Similarities subtests from the WAIS-R ($N = 78$) [59]. The Primary Mental Abilities Vocabulary Test (VOCAB) is a test of verbal knowledge and vocabulary. The participant is asked to select, from four alternatives, the word which is most similar in meaning to a target word. A time limit of three minutes for completion of the 50 items is given. Vocabulary performance is highly correlated with measures of psychometric intelligence [59], and this measure was included to assess general cognitive function. The dependent variable was the total number words correct minus one-third the number incorrect. The California Verbal Learning Test (CVLT) was administered as a measure of verbal learning and memory of a list of 16 target words. In this study, the dependent measures used were the total number of words recalled across the 5 learning trials (CVLTA), the total number of words recalled following a long delay (CVLTLD) and the recognition discriminability (CVLTDIS), a measure of the participants' ability to discriminate between targets and distractors on a recognition test. The Benton

Visual Retention Test ($N = 84$) is a test of short-term visual memory. In each of 10 trials, the participant views a figure for 10 s. Following the removal of the figure from view, the participant attempts to draw it on a blank sheet of paper. The figures are scored for errors according to established criteria [8], and the dependent variable was the total number of errors committed over all 10 figures. The Card Rotations Test is a test of mental rotation. On each of 28 trials, the participant is presented with a target figure and 8 other similar figures to the right of the target. Some of the 8 figures are the same as the target figure except that they have been rotated in the picture plane and other figures are different (mirror images which have been flipped over). For each of the figures, the participant must indicate whether the figure is a rotated version of the target or mirror image of the target. The dependent measure was the total number of items correct minus the total incorrect, summed over 2 parts (CRT). The Digit Span subtest of the WAIS-R served as a measure of short-term memory and attention/concentration. In the forward Digit Span subtest (DIGFOR), the participant is read aloud a series of digits and must repeat back those digits in the same order. In the Backward Digit Span subtest (DIGBAC), administration is as for digit span forward with the exception that the participant must repeat the digits backwards. In addition to the attentional component, DIGBAC taps working memory processes, as mental manipulation of the digit string is required for successful performance. In both DIGFOR and DIGBAC, the digit string gets progressively longer with each correct answer. Scoring was performed using the standard WAIS-R scoring criteria [59]. The Similarities subtest of the WAIS-R served as a measure of abstract verbal concept formation. The participant is presented with 13 pairs of words and must explain how each pair are similar. Scoring was according to WAIS-R scoring criteria [59].

3. Results

To examine the effects of age on VE navigation, several analytic approaches were utilized. In the first series of analyses, age was treated as a continuous variable and entered into 3 separate multiple regression analyses to examine completion time, distance, and errors, separately. In each regression analysis, age, sex, joystick visuomotor control, and computer experience were entered simultaneously as independent variables to predict the dependent measure. The first analysis examined the effect of the independent predictors on total time required to complete all five trials. These factors predicted a substantial proportion of the variance in maze completion time [R = .63, F (4,110) = 18.09, $P < 0.001$]. As shown in Table 2, there were significant effects of age with younger participants solving the maze faster than older participants, sex with males faster than females, computer experience with individuals having more computer experience showing faster maze times than those with more limited experience, and a positive effect of joystick motor control speed. The salient result from this analysis is the substantial effect of age, independent of age-related and other variability associated with differences in computer experience and visuomotor control. When a similar analysis was conducted with total distance traveled over the 5 trials as the dependent variable, only the effect of age was significant [R = .438, F(4, 110) = 6.52, $P < 0.001$] (see Table 2).

Table 2
Multiple regression results

Model	Standardized Beta	T	P
Dependent variable: Total time to completion			
Age	.341	3.48	.0007
Sex	.150	1.95	.054
Joystick control	.239	2.75	.007
Computer experience	−.189	2.13	.035
Dependent variable: Total distance traveled			
Age	.402	3.53	.0006
Sex	.114	1.28	.203
Joystick control	−.090	0.90	.370
Computer experience	−.128	1.25	.215
Dependent variable: Total number of spatial memory errors			
Age	.414	3.68	.0003
Sex	.180	2.04	.044
Joystick control	−.064	0.64	.522
Computer experience	−.111	1.09	.278

Analysis of the effects of the independent predictor variables on the total number of spatial memory errors committed indicated that only the effects of age and sex reached significance [R = .46; F(4,110) = 7.28, $P < 0.001$]. Older participants made more spatial memory errors than younger participants, and females committed significantly more spatial memory errors than males. Neither the amount of computer experience nor performance on the visuomotor joystick control test predicted the number of spatial memory errors committed during navigation.

For repeated measures analyses of learning over the 5 trials, participants were divided into young (<45.0 years), middle (45.1 to 65.0 years), and old (>65.1 years) age groups. To examine age and sex effects across the 5 trials of the maze, a repeated measures ANOVA was performed with Sex and Age Group as independent variables and time to completion on each of the 5 trials as the dependent variable. There was a main effect of trial indicating that participants solved the maze in less time on each subsequent trial [F(4, 108) = 14.72, $P < 0.001$], a main effect of age [F(2,111) = 25.49, $P < 0.001$] with older individuals slower overall, and a trend toward an effect of sex [F(1,111) = 3.45, $P = 0.07$] with men faster than women. There were no significant interactions, indicating that learning slope over repeated

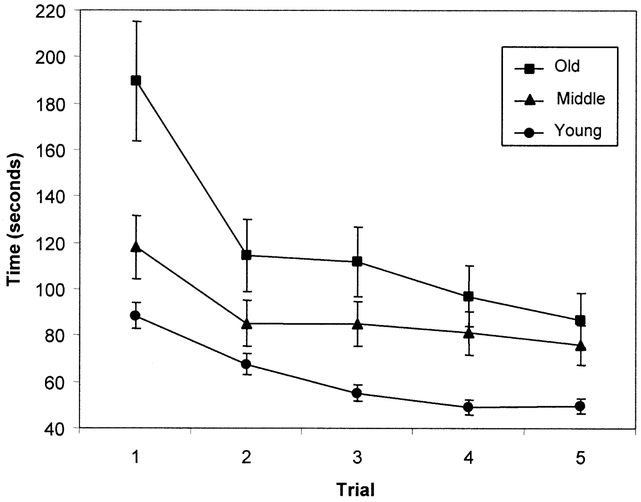

Fig. 1. Time required to complete the maze as a function of age group and trial. All age groups showed reductions in the time required to solve the task on each trial. However, older participants took longer to solve the maze on each trial than their younger counterparts.

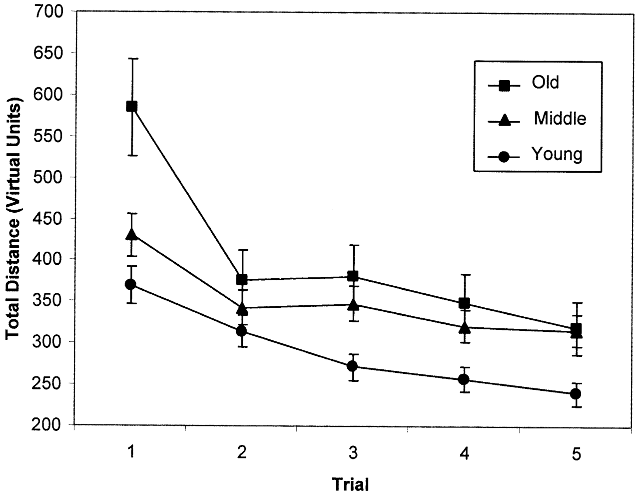

Fig. 2. Total distance traveled as a function of age group and trial. All age groups showed reductions in the distance traveled on each subsequent trial. Overall, younger participants traveled a shorter linear distance than their older counterparts.

trials was similar for younger and older participants and for men and women. Fig. 1 shows the age differences in completion times across maze learning trials. Tukey HSD post-hoc tests of the main effect of age revealed that the youngest age group was faster than both of the older age groups (p's $< .002$), and the middle age group solved the maze faster than the oldest age group ($P < 0.001$). For repeated measures analysis of total distance traveled on each of the five trials, there were main effects of trial [$F(4,108) = 13.95$, $P < 0.001$] and age [$F(2,111) = 11.62$, $P < 0.001$]. Post hoc tests revealed that the youngest age group traveled less distance than the middle ($P < 0.02$) and the oldest age groups ($P < 0.001$). There was a trend ($P < 0.08$) for the middle and oldest age groups to differ (see Fig. 2).

Repeated measures analysis of the total number of spatial memory errors committed across trials revealed significant main effects of trial [$F(4,108) = 3.01$, $P = 0.021$], and a main effect of age [$F(2, 111) = 12.47$, $P < 0.001$]. There were no significant interactions. Tukey HSD post-hoc tests of the main effect of age revealed that the youngest age group committed fewer spatial memory errors than both of the older age groups (p's $< .007$). The middle and oldest age groups did not differ significantly ($P = 0.17$). An additional analysis was performed on the number of trial 1 information errors to determine whether age and sex influenced initial exploratory behavior in the maze. A Sex by Age ANOVA with total number of information errors as the dependent measure yielded no significant effects of age [$F(2,111) = 1.44$, $P = 0.24$] or sex [$F(1,111) = 0.49$, $P = 0.49$], as expected. Fig. 3 shows an overhead perspective of the path followed over 1 trial by a representative young and representative older participant.

It was also of interest to examine the proportion of participants who were able to learn the layout of the environment to criterion performance level over the 5 trials. To address this, we performed a chi square analysis comparing the frequencies of participants in the young, middle and old age groups who were able to solve the maze without error by the fifth trial. Eighty-six percent of the young participants, 51% of the middle aged and 24% of the oldest participants were able to solve the maze without error by the fifth trial [$\chi^2 = 26.77$, $P < 0.001$].

To examine the relationship between maze performance and the cognitive test scores, partial correlations controlling for age were performed. For the maze learning task, the total time to completion, the total distance traveled, and the total number of spatial memory errors committed over all five trials were used as summary variables. As shown in Table 3, there were consistent and selective positive correlations between virtual maze learning and the verbal memory measures of immediate free recall, delayed free recall and recognition discriminability. Positive correlations were also observed between the navigation task and measures of visual memory, and mental rotations performance. This was consistent across the time, distance and error measures of maze performance. None of the other cognitive tests showed significant correlations with maze learning performance.

4. Discussion

The results of the present study demonstrate that VE technology can be used to assess age effects in route learning. The performance of young, middle and older individuals improved with each trial in the maze, showing a reduction in time to completion, distance traveled and the number of errors committed. However, despite improvement in performance as a function of trial, elderly individuals were clearly impaired in overall performance relative to the younger age groups. The number of spatial memory

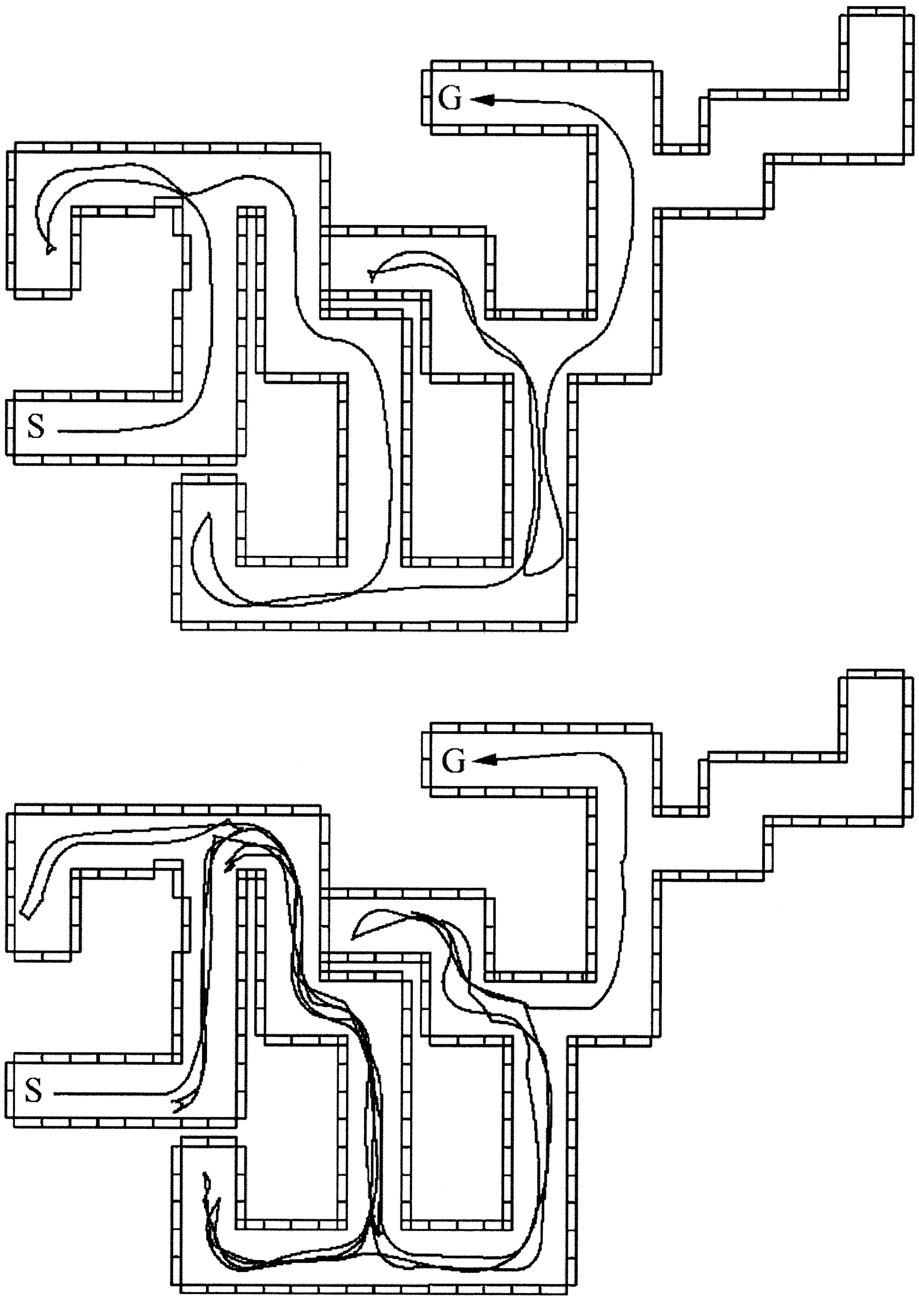

Fig. 3. Overhead plot of the path traveled by 1 young (top panel) and 1 old (bottom panel) subject on their first trial in the maze, illustrating information and spatial memory errors committed. The young subject was a 33 year old male who committed 3 information errors and 1 spatial memory error on this trial. The elderly subject was an 81 year old male who committed 3 information errors and 6 spatial memory errors. Overall, older subjects made more frequent repeat visits to previously visited error locations, took longer to solve the task and traveled a longer linear distance before locating the goal (G – goal; S – start box). However, younger and older individuals did not differ in the number of information errors committed.

errors committed, the distance traveled, and the time required to complete the maze increased with age. Elderly volunteers made more frequent repeat visits to previously visited error locations that they should have remembered from previous experience to be dead ends. Moreover, after 5 trials in the maze, 86% of young and only 24% of the oldest volunteers were able to complete the maze without error. Importantly, there were no age differences in trial 1 information errors indicating that the age groups were well-matched in their initial exploratory behavior of the environment. Thus, it was only the tendency for older individuals to make repeat visits to error locations that differentiated the age groups.

The age differences observed in our study were not

Table 3
Partial correlations controlling for age between navigation performance and psychometric measures of cognition

	Maze time$^+$	Maze distance$^+$	Spatial errors$^+$
VOCAB	−.079	−.104	.133
BVRT$^+$	.345**	.235*	.276*
CVLTA	−.260*	−.290*	−.297*
CVLTLD	−.344**	−.288*	−.334**
CVLTDIS	−.367**	−.367**	−.441**
CRT	−.301**	−.306**	−.307**
SIMILAR	−.159	−.192	−.210
DIGFOR	.034	−.072	−.023
DIGBAC	−.288*	−.190	−.197

$^+$ Scoring scale reversed: higher scores denote poorer performance.
** $p < .01$
* $p < .05$
[Abbreviations: VOCAB, PMA Vocabulary Test; BVRT, Benton Visual Retention Test; CVLTA, California Verbal Learning Test, Immediate Free Recall of 5 Trials of List A; CVLTLD, California Verbal Learning Test, Long Delay Free Recall; CVLTDIS California Verbal Learning Test, Recognition Discriminability; CRT, Card Rotations Test, SIMILAR, WAIS-R Similarities Subtest; DIGFOR, WAIS-R Digit Span Forward Subtest; DIGBAC, WAIS-R Digit Span Backward Subtest].

simply a function of lack of computer experience and generalized psychomotor slowing in the elderly. All participants were given training on the use of the joystick and were required to satisfactorily complete a timed speed test prior to maze navigation testing. In our regression models, significant age effects were observed after adjustment for the effects of computer experience and joystick visuomotor control. The latter variables accounted for a significant proportion of variance in time to completion but had no detectable effect on the distance traveled and the number of spatial memory errors committed. It appears that having considerable experience using a computer engenders a certain fluency in the human-computer interaction resulting in faster completion times, but does not result in a facilitation of spatial memory per se. This suggests that the error measures employed in the present study are not contaminated by age differences in computer competence and psychomotor processing speed. It is important to point out that even when using time as a dependent measure, the age effect on the task was substantially greater than may be accounted for by age differences in computer competence or more general declines in visuomotor processing (see Table 2). Nevertheless, general age differences in computer experience and psychomotor processing speed should be taken into account for VE tasks relying on completion time as the primary dependent measure.

One limitation of the present study is that approximately 10% of participants experienced some degree of nausea and dizziness associated with this relatively brief desktop VE exposure, resulting in the withdrawal of 13 participants from the study. Participants withdrawing from the study differentially consisted of older females (see “Participants”), but were comparable to the remaining participants in years of education and cognitive test scores (p’s $> .05$). Nausea and dizziness have been reported as side effects from VE immersion [22,47], and previous research has noted that females are more likely than males to experience dizziness from VE exposure [55]. We are not aware of studies comparing older and younger participants in their susceptibility to VE-induced nausea. However, it is well-known that the incidence of dizziness from a variety of sources increases with age [57]. We believe that some elderly participants may be particularly sensitive to the discrepancy between visual and vestibular/proprioceptive sensations that is believed to underlie VE-induced motion sickness. Despite this subject withdrawal, it is important to emphasize that this feature did not substantially compromise the validity of our findings. The withdrawal of older females likely served to *minimize* the observed age and sex differences rather than to create differences which were not real.

Prior studies of navigation in elderly humans have demonstrated that older individuals show objective route learning and navigation impairments [26,27,41,61] and have increased avoidance of unfamiliar routes and places [10]. In Alzheimer’s Disease, wandering away from home and becoming lost is common and extremely troublesome for patients and caregivers alike [28,46]. Ecological studies of age-differences in spatial learning are rare primarily because of the practical difficulty associated with testing. It is difficult to gain control over the location and placement of landmarks in the real world, and insofar as testing the elderly is concerned, physical impairments may limit their ability and willingness to traverse routes over the repeated trials necessary for assessment of learning curves.

The greatest advantage afforded by VE testing is that it gives the experimenter unlimited control over the visual features and complexity of the environment, allows detailed recording of behavioral responses to be automated, and allows landmark and route manipulations which could not easily be accomplished in the real world. However, the question also arises as to what extent VE testing simulates real world navigation and depends upon similar behavioral and neural mechanisms. Clearly the greatest drawback of desktop VE testing is that it does not involve actual movement through space. This restricts coverage of the visual field and deprives the participant of vestibular, kinesthetic and proprioceptive cues which are used to help maintain course in the real world [9,44]. VE testing assesses only that component of navigation or route learning which is visually-based with an absence of sources of input from other sensory systems.

Despite these limitations, recent studies suggest that the spatial knowledge acquired through learning in a VE transfers well to subsequent navigation in the real world [2,62]. For example, training participants on a virtual version of the Kiel locomotor maze enhanced subsequent acquisition of the actual maze [17]. Participants made accurate and confident responses in the real maze as a consequence of having received training in virtual space. Moreover, Ruddle et al. (1997) found that participants develop ‘cognitive maps’ in a VE that are similar to the maps derived from exploration of the real world [49]. Our results suggest that the assessment of spatial navigation in the elderly may be an important application of VE technology that will enable researchers to understand age differences in route and place learning as well as possible age-differences in the utilization of landmarks and cues.

The majority of investigations into age changes in human memory have focused on verbal list learning or the recall of geometric figures or patterns. These memory measures have marked task differences from the measures typically used to assess mammalian spatial memory. Spatial memory tasks in rodents, birds and in some studies of non-human primates involve paradigms requiring actual navigation through or perception of three dimensional space and thus, generate theoretical models which emphasize spatial computation. In studies of human memory function and cognitive aging, the reliance on psychometric measures of cognition (e.g. list learning, figural recall) tends to elicit models emphasizing episodic memory and the distinction between multiple memory systems. Nevertheless, researchers will frequently make reference to findings from electrophysiological, pharmacological and lesion-based studies derived from the animal literature and apply this perspective to research on humans performing tasks which, superficially at least, appear to require different information processing demands.

The observation of significant correlations between VE navigation and selected psychometric tests addresses directly the behavioral overlap of VE navigation tasks with other cognitive domains. Performance on the spatial maze learning task was predicted only by measures of visual and verbal memory and spatial rotational ability. Other cognitive tests such as vocabulary, complex verbal reasoning and attention/concentration were not predictive of maze learning performance. VE navigation is a complex perceptuo-cognitive behavior which presumably shares some selected cognitive processing modules in common with other traditional measures of cognitive aging. These results may provide preliminary evidence for common neural systems mediating at least some mutually compatible components of these seemingly disparate cognitive tasks. The fact that we used repeated trials in which participants were required to learn and remember a route likely placed considerable demands on an explicit memory system resulting in a positive correlation between maze learning performance and episodic visual and verbal memory scores. Moreover, the requirement to remain unconfused by changes in direction and orientation within the VE may exploit spatial problem solving systems similar to those tapped by measures of mental rotation or other complex visuospatial cognitive tasks. It is important to emphasize, however, that the correlations were small to moderate in magnitude. Thus, in addition to shared variance with traditional cognitive tasks, the navigation task also involves unique information processing demands which were not sampled by any of our psychometric cognitive tests. These findings indicate that the navigation task may yield unique information on the nature and implications of age differences in spatial learning and memory.

In non-human species, senescence is associated with marked route learning [23] and place learning deficits [5,35]. In the rodent hippocampus, a structure whose integrity is necessary for successful navigation [39], cellular, pharmacologic and metabolic changes associated with aging may underlie the observed spatial learning deficits [18]. Moreover, hippocampal place cells show age-related changes in their firing patterns which may underlie the age differences in spatial learning [6,7,51]. In the monkey, cells in the hippocampus have been identified that respond to spatial location [33,42] and spatial views of the environment [19,48], but there are no studies of age effects on the response properties of these cells.

In humans, recent neuroimaging studies employing VE technology have demonstrated the existence of a navigational network which is activated while participants attempt to find their way through virtual environments. Virtual navigation tasks in PET and fMRI have revealed brain activation in the hippocampus, parahippocampal region, inferior parietal cortex, precuneus and other regions [1,21,30]. Because some of the structures which appear to play a prominent role in human navigation are also vulnerable to age-related neurodegenerative processes [24,60], it seems plausible that age-related navigational deficits may be one behavioral manifestation of any of a variety of associated neurological changes. Future studies will investigate whether young and elderly participants may show a different magnitude or different patterns of neural activation in VE route or place learning tasks. The present results provide the behavioral foundations for understanding the neural mechanisms of age-related declines in human spatial cognition.

The purpose of this study was to design a task which is similar in several respects to those measures of cognitive aging which are used in non-human species, and to provide data on the interrelationships between this navigational measure of spatial memory and more traditional cognitive tasks that are in widespread use in clinical and research settings. If VE technology is incorporated to promote a functional, anatomic and evolutionary understanding of human navigation, it is essential that we quantify the behavior of both young and old participants in virtual space and examine the interrelationship with supplementary measures of cognition. The application of VE spatial learning tasks in behavioral and neuroimaging studies may foster more precise comparisons between human and non-human species and facilitate a comparative approach to the neuroscience of cognitive aging.

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