

RESEARCH ARTICLE

Using Virtual Reality to Investigate Comparative Spatial Cognitive Abilities in Chimpanzees and Humans

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The purpose of the present study was to determine the efficacy of investigating spatial cognitive abilities across two primate species using virtual reality. In this study, we presented four captive adult chimpanzees and 16 humans (12 children and 4 adults) with simulated environments of increasing complexity and size to compare species' attention to visuo-spatial features during navigation. The specific task required participants to attend to landmarks in navigating along routes in order to localize the goal site. Both species were found to discriminate effectively between positive and negative landmarks. Assessing path efficiency revealed that both species and all age groups used relatively efficient, distance reducing routes during navigation. Compared to the chimpanzees and adult humans however, younger children's performance decreased as maze complexity and size increased. Surprisingly, in the most complex maze category the humans' performance was less accurate compared to one female chimpanzee. These results suggest that the method of using virtual reality to test captive primates, and in particular, chimpanzees, affords significant cross-species investigations of spatial cognitive and developmental comparisons. *Am. J. Primatol.* 76:496–513, 2014. © 2014 Wiley Periodicals, Inc.

Key words: virtual reality; chimpanzees; humans; spatial cognition; small- and large-scale environments; landmarks

INTRODUCTION

Navigating among multiple locations within a home range, animals must be able to discriminate, track, and integrate salient spatial cues when generating effective strategies for route taking and identifying goal sites. Environments of different scale may affect navigational strategies. Thus in small-scale space that affords a visual overview of landmarks [Poucet, 1993], traveling between nearby locations represents a different set of navigational challenges than in large-scale space where locations and landmarks are not visible from one to the next. Scale may equally affect differences in the generation of internal representations of space such that small- and large-scale environments may be represented accordingly, either topologically (encoding of exaggerated distance, angle, and direction, with corrections re-adjusted at known sites, nodes, during navigation) or metrically (encoding of actual distance, angle, and direction among multiple landmarks) [Dolins & Mitchell, 2010; Maguire et al., 1997]. Moreover, experience in navigation within an environment, as found with humans and other primate species, may affect the generation of internal spatial representations, efficiency of travel, and type of spatial strategy applied in a particular type of environment [Asencio

et al., 2011; Beeson et al., 2010; Byrne & Janson, 2007; Dolins, 2009; Dolins & Mitchell, 2010; Garber & Dolins, 2010; Healy & Braithwaite, 2010; Maguire et al., 1997]. Additionally, in the case of wild primates, their knowledge of foraging sites must interface with current ecological factors, such as availability of fruit and seasonal variations of items for consumption. Assessments must account for how these factors affect navigation [Janmaat et al., 2013]. In sum, major issues that researchers face in the study of spatial

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Francine Dolins dedicates this paper to Merry, Brandy, and Domani, and to the memory of her good friend, Alan Cowey.

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cognition are identifying what specific visuo-spatial information forms the basis of spatial strategies and internal representations, and how scale and experience may interact with these factors. Given these significant methodological challenges, using a controlled experimental setting via virtual reality, we can assess and identify navigational strategies, attention to landmarks, influence of ecological factors, and efficiency of travel.

There is a trade-off between the ecological validity and experimental control when conducting studies with captive or wild primates. In many free-ranging spatial-foraging studies, researchers encounter difficulties assessing which landmarks are salient to the navigating animal [e.g., Garber & Dolins, 2010]. In captive studies, small-scale space and limited ecological validity are issues with being able to generalize the results to the wild population of that species. Results from captive studies investigating spatial strategies in small-scale space, which have limited ecological validity, are problematic to generalize to the behavior of wild counterparts. A successful robotics approach has melded spatial scale of environments and control over landmark presentation. This approach uses initial exploratory behavior compared with that developing from the coded spatial information to determine whether metric or topological strategies have been applied in navigation to a location [Beeson et al., 2010]. However, with real animals, to overcome these methodological difficulties, we have developed a virtual reality (VR) software program to simulate environments of varied landmark features, scale, and complexity to human and nonhuman primates. VR has the capacity to present some degree of ecologically valid spatial scenarios. Greater experimental control over potential landmarks and geometry of space can also provide more precise assessment of attention to the various topographical features. Thus, VR assists in creating an experimental situation where both ecological validity and control over variables (e.g., landmarks) affords while simultaneously presenting environments that can vary in features, scale and complexity [e.g., De Lillo & James, 2012].

The study described in this paper uses VR as a method to investigate spatial cognitive abilities of a nonhuman primate species, in particular chimpanzees. We used a comparative approach and tested the performance of both humans and chimpanzees to assess their relative ability to navigate in virtual space and their relative attention to and discrimination of landmark types. VR offers flexibility in creating varied environments by factors of scale and complexity, populated with 2D and 3D landmarks. Simulations also afford presentation of either built or naturalistic environments, the latter to enhance ecological validity.

One of the key issues in establishing VR as a viable methodology to study primate spatial cognition

is whether nonhuman primates will perceive virtual space similarly to that of human counterparts. This raises the question about degree of ecological validity of the visuo-spatial experience in virtual environments for nonhuman primates. A virtual environment is by default a two-dimensional (2D) presentation, although perceived and utilized by most humans as a three dimensional (3D) space populated with objects, geometry, topographical features, and landmarks. Evidence for chimpanzee perception of 3D objects presented in a 2D format (e.g., a computer monitor) has been demonstrated by testing visual search tasks of 3D images of objects presented against a visual ground [Imura & Tomonaga, 2007]. In parallel with human performance, the chimpanzees clearly demonstrated visual search patterns commensurate with the distribution of 3D depth-cues against the background, with emphasis on a ground dominance effect, defined for both species as using ground, walls and ceiling as anchors for visually investigating forward-perceived features [Bian et al., 2005]. A study tracking chimpanzees' and humans' eye movements to animal whole-body images presented on a 2D computer monitor (e.g., pictures of a chimpanzee, human, and other mammal) reveals that viewing patterns and eye-movement strategies maintain significant similarities for both species [Kano & Tomonaga, 2009]. Significantly, the chimpanzees showed attention directed initially to faces but for longer durations to other body parts than human counterparts, who focused for a greater duration on faces [Kano & Tomonaga, 2009]. Compared to humans, the chimpanzees' eye movements displayed patterns of shifting fixation more regularly and rapidly, and to increased locations on the stimulus. Overall however, the results demonstrate the close similarity of chimpanzees' and humans' visual perceptual strategies and eye movements on visuo-spatial information presented in a 2D format.

In the present series of experiments using virtually simulated environments of increasing complexity (determined by numbers of landmarks and choice points), relative scale, and closed versus open space, our objective was to determine how efficiently chimpanzees could navigate and whether chimpanzee performance in a virtual 3D environment presented on a 2D medium (a computer screen) would differ from that of human performance. The performance measure for both species is based on actual distance traveled from start to goal compared to an optimal-generated distance. We also aimed to evaluate where, within a developmental framework, chimpanzee performance was most equivalent within human age trajectories and so we tested children of three age groups (3 to 4, 5 to 6, and 11- to 12-year olds) and adult humans (38–48 years).

Specifically, our goals were to determine whether (1) chimpanzees and humans would respond similarly to a 2D presentation of a 3D environment in terms

of success in localizing the goal, decisions at choice points, and latency to achieve the goal; (2) chimpanzees and humans would similarly attend to and discriminate between positive (“go”) and negative (“don’t go”) directional cues presented in the virtual environments; and (3) increasing complexity (number of directional visual landmarks) and size of environment would impact the performance of the chimpanzees and humans. Additionally, when either the goal or the starting position is altered per trial in a complex maze environment while the remainder of the environment remains fixed over trials, would this level of spatial complexity result in differences in chimpanzee and human performance?

METHODS

Each set of experimental conditions presented a different environment type. The objective for the navigator was to attend to the directional cues provided by the landmark (positive or negative) to successfully localize the goal. The presentation of positive and negative landmarks requires the individual to discriminate between the landmarks as directional cues. With only two landmark types, positive and negative, presented in each environmental design (maze or open space) and the goal randomized per trial, this study aims to test reliance on landmarks and not recall of pathways (right and left turns) by kinesthetic feedback. Additionally, to achieve success (localize the goal) the navigator was not *required* to learn the geometric format of these environments, which would be commensurate with a metric mapping representation; however, doing so may enhance their success [Dolins, 2009]. Sensitivity and attention to the nature of the landmarks and their meaning provides directional information. Salience of landmarks and featural information can be defined as the extent to which a particular landmark is attended to and used by the traveling individual, and which becomes learned as a substantive directional feature upon which active spatial decisions will be made in choosing a route [Dolins & Mitchell, 2010; Lipman, 1991].

Latency to localize the goal, path length traveled, and paths/path directions selected at choice-points (T-junctions in the mazes) were measured in each of the virtual environments. It was predicted that as individuals gained experience with the directional cues, even in more complex environments, their latency and path length would decrease, and decisions at choice-points would become more accurate, with fewer instances of backtracking to localize the goal.

We conducted a series of experiments with four chimpanzees and 16 human participants presenting three types of virtual environments of increasing complexity including (A) T-mazes with consistent start and randomized goal locations, (B) open space

designs with the goal hidden behind one or two barriers, and (C) complex, large environments composed of multiple alleyways with either randomized start and consistent goal locations, or vice versa. In all three types of environments the same two landmark types presented were either *positive* (2D blue square representing “go” or “correct direction”) or *negative* (2D brown triangle representing “don’t go” or “incorrect direction”). In each environment the goal stimulus was a 2D image of a tree and 3D green ball and when the on-screen cursor (a moving arrow directed by the joystick) connected to either, a ring tone was produced signaling successful completion of the task (see Fig. 1).

Participants and Research Sites

Four adult chimpanzees (Lana, Mercury, Panzee, and Sherman) housed at The Language Research Center, Georgia State University, were trained and tested using the virtual maze and open space environments in the familiar laboratory setting. At the time of testing, Lana was 37 years old, Mercury was 21 years old, Sherman was 34 years old and Panzee was 22 years old. Trained research technicians highly proficient in working with chimpanzees conducted all computerized tests. All four chimpanzees have extensive experience in working cognitive and perceptual tasks on joysticks and computers and exposed to a language-rich environment [Rumbaugh & Washburn, 2003]; three have been symbol-referent trained on the lexigram board. These chimpanzees were willing to work on the task as soon as they were given access to the joystick apparatus.

Sixteen humans participated in this study in Winchester, England. Twelve children, equal male and female, aged 3–4 ($n = 4$), 5 to 6 ($n = 4$), and 11 to 12-years ($n = 4$) and four adults (two males 43 and 49 years old, two females 38 and 48 years old) were tested on the same experimental VR designs as those presented to the chimpanzees. Participants were tested in their homes or a familiar environment. Each parent or guardian signed consent forms for their child to take part in the study, and during testing a parent or guardian always was present.

All animal care, housing and testing procedures complied fully with Georgia State University’s Animal Care and Use Committee and with that of the USDA regulations on animal care and welfare. All research reported in this manuscript adheres to the American Society of Primatologists’ (ASP) principles for the ethical treatment of primates. Testing of all human participants complied fully with the ethical standards set by the UK Home Office.

Materials

In addition to the specially designed virtual reality program (more details below), an Apple

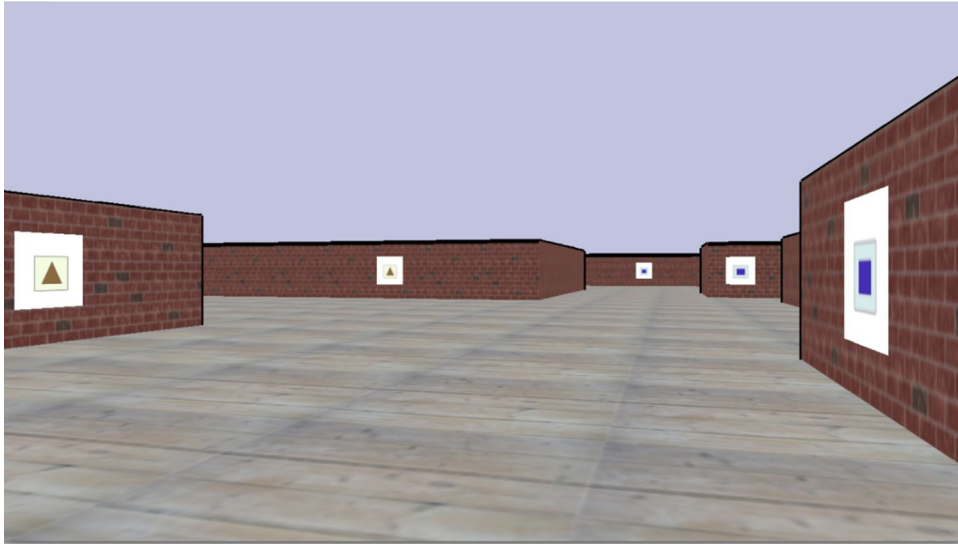


Fig. 1. This figure presents a navigator's view interior to a virtual environment. On the virtual walls, the brown triangles are negative landmarks and blue squares are positive landmarks.

computer, 20-in. flat screen monitor, and joystick were used in testing both chimpanzees and human participants. Positive, automated auditory feedback and food rewards were given to the chimpanzees when localizing the goal (the food rewards were not automated in delivery but given by hand). Children and adults were given verbal rewards during testing when reaching the goal, and presented with a small token gift (children received colorful stickers or pencils; adults received book certificates to a national bookstore chain) at the end of the test session.

Virtual Reality Program

The virtual reality program, written in C++ and OpenGL, allows presentation of a geometrically based landmark environment. Figure 1 presents a navigator's view interior to a virtual environment. The VR program presents high-quality visual environments for training and testing. It allows flexible design of each environmental design such as placement of T-junctions in mazes with distinct choice points. The program also allows presentation of virtual open space environments with large open areas that vary in scale and placement of barriers/walls. The program automatically records position and orientation in 3D space on a frame-by-frame basis to allow the independent variables of performance such as path length, latency from start to goal, and overall distance, to be accurately measured and analyzed.

The VR program enables presentation of sequences of environmental designs (e.g., mazes) for automated trials during testing. In testing, when

participants reached criterion performance (success on 80% of all trials for one environmental design), the program automatically shifted to the next environmental design. These were pre-set in randomized or specific order depending on training or testing requirements. It was possible to designate the start position in a VR environments as either north, south, east or west. The virtual cardinal directions were designated according to the following: north = "joystick up," south = "joystick down," east = "joystick right," and west = "joystick left."

Virtual T-Mazes and Open Space Designs Presented for Training

We presented participants with a minimum of 10–20 training trials; however, some of the younger children did not complete all training trials, requesting to stop. The chimpanzees were given 5–10 training trials on the simple straight alleyway prior to some test sessions as a reminder of the task. Training trials on mazes presented a straight-alley maze (one alleyway, fixed start position, goal visible) and then a straight-alley maze (one alleyway, fixed start position, goal visible, two positive landmarks proximate to the goal). Training trials on the virtual open space design (arena with eight possible goal locations), presented an open arena surrounded by boundary walls (with no additional visible barriers), a fixed start position and the goal located randomly in one of eight locations around the perimeter of the walls. Figure 2 represents an open space design (with one of the eight random locations of goal on perimeter) used for training.

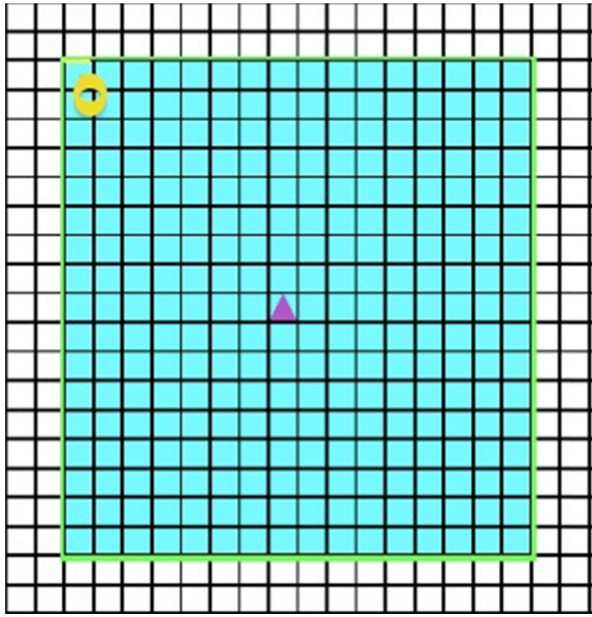


Fig. 2. This figure represents an open space design (with one of the eight random locations of goal on perimeter) used for training. The yellow circle in the upper right hand corner represents the location of the goal on this trial, while the pink triangle is the constant start position, always facing north.

Virtual T-Mazes Presented for Testing

The mazes presented during testing were 1T-, 2T-, and 3T-mazes each with a fixed start location but a randomized goal location during each trial. The goal location was always at the end of a distal alley. Correspondingly, for the navigator the 1T-maze afforded one choice-point, the 2T-maze afforded three choice-points, and the 3T-maze afforded five choice-points. The 3T-maze was designed not to be symmetrical in order to keep complexity to a reasonable level. Figure 3a–c present diagrammatic representations of the three types of VR T-maze environments, 1 T-maze, 2 T-maze and 3 T-maze.

Virtual Open Space and Complex Maze Designs Presented for Testing

In the open space designs the goal was not visible from the start. It was hidden behind one of two opaque barriers designated by either positive or negative landmarks. The participant's movements were not restricted to T-alleys. Nevertheless, the space contained barriers to movement and seeing. In the complex multi-alley maze environments the same fixed alleyways were present on every trial but varied with either a random start + fixed goal location, or a fixed start + random goal location, per trial. The goal and most of the landmarks and alleyways were not visible from the start position.

Figure 4a–d present diagrammatic representations of the four types of VR open space designs used in testing. In the first open space test design, one 3D

barrier was located to occlude the view of the goal. Two positive landmarks were placed on the perimeter wall, visible either side of the barrier. The “barrier + 2 landmarks + goal” array (one-barrier design) was set randomly, per trial, around the perimeter of the arena in one of four locations. The second open space design presented two barriers. The goal was located behind the barrier with adjacent positive landmarks, while the other barrier had two adjacent negative landmarks. The locations of the two barriers were randomized around the perimeter of the four walls, so that in two conditions (A and B) the barriers maintained a visual and spatial proximity, while in other conditions they were separated on opposite sides of the arena (C and D). The direction of the start position (facing either north, south, east or west) was randomized over trials. In the third design, large visual barriers were constructed to create a complex set of alleyways; the start position was fixed and goal location randomized over trials. Positive/negative landmarks acted as guides to the location of the goal. In the fourth design, using the same construction of barrier + alleyway design, the start position was randomized over trials while the goal location was fixed.

Data Collection

Data generated by the virtual reality program are automatically recorded in separate text files, per trial and per subject/participant. Each text file contains a navigator's movements in X, Y coordinates recorded per millisecond. Prior to training, the 3 to 4 and 5- to 6-year-old children were given time to acclimate to using a joystick to be able to monitor movement of the cursor on a blank screen.

Training for participants occurred in one session. Chimpanzee and human participants were presented initially with a straight-alley maze for at least 20 trials. On the virtual open space design, participants were presented with an open arena where the start position was fixed however the goal was in one of eight locations (randomized) around the perimeter of the walls for up to 20 trials (see Fig. 2 for diagrams of these environments). All 4 chimpanzees and 16 human participants achieved an approximately equivalent level of proficiency in both the training alleyway and open space design prior to testing. Criterion for all trials was reached when participants localized the goal in 25 sec or fewer on 18 of 20 (or 90%) on successive trials (with no fixed number of trials per individual; 20 trials was equivalent to one session). Participants were given the opportunity to complete a sequence of trials of maze or open designs for that session (details later).

General Testing Procedures

On the same or consecutive days after training, all participants were given the opportunity to be

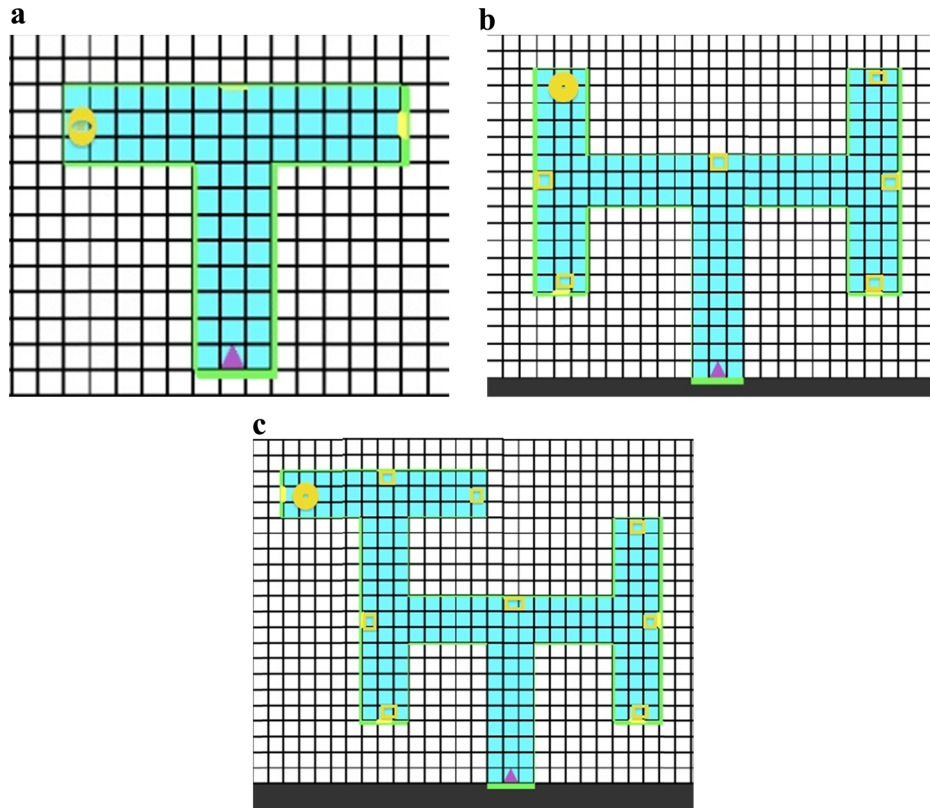


Fig. 3. These three figures present diagrammatic representations of the three VR T-maze environments used in testing the chimpanzees and human participants, comparatively. The pink triangle symbolizes the start position and direction of view on beginning a trial. The yellow squares symbolize the landmarks; the goal is represented by a yellow circle. (a) A diagram of one of the two versions of the VR 1 T-maze used in testing subjects and participants (goal location randomized in T-maze at the end of either the right or left alleyways). (b) A diagram of one of the four versions of the VR 2 T-mazes used in testing subjects and participants (goal location randomized in the T-maze at the end of one of the four alleyways). (c) A diagram of one of the four versions of the VR 3 T-maze used in testing subjects and participants (goal location randomized in T-maze at the end of one of the five alleyways).

tested on all three virtual T-mazes (1T-, 2T-, and 3T-mazes), the open space environment designs, and the complex maze (multi-alley environment). In all virtual environments presented, positive landmarks were aligned with the correct route to the goal, while negative landmarks were spatially associated with one of the incorrect routes. In the T-mazes, the landmarks were located at either end of the alleyways. Each testing session consisted of up to 20 trials presenting randomized (per goal location) designs of a given type of environment.

Depending on the age of the participant and the attention span per age, different numbers of trials were completed per VR environment type (see Table I for specific numbers of trials completed by each subject and human participant in each environment type). Criterion for all experiments was achieved when the participant reached the goal in 16 of 20 trials (80%). If participants did not achieve the goal in 2 min or less, a trial was considered unsuccessful.

Testing Procedures

Prior to testing, the chimpanzees were asked individually if they wanted to “work.” If they agreed,

they positioned themselves in front of a Plexiglas workstation where they could see a computer monitor and reach a joystick (encased in a port hole for safety) to manipulate from their sitting position. A research technician was positioned outside the wire mesh of the cage (3–5 feet distance), unable to see the screen and therefore unable to influence performance. At the start of each session, the technician initiated the VR program sequence. The program ran through a pre-specified series of tests automatically until either all the tests were completed or the subject showed inattention or frustration whereupon the testing session was terminated; the technicians tried to regain a subject’s attention at a later time to complete the trials. In the case of humans, prior to testing, the experimenter explained to participants that they would be asked to use a joystick to navigate around an environment. The experimenter initiated the sequence of trials and positioned herself where she was unable to see the screen and therefore unable to influence performance. For both humans and chimpanzees, the program presented a pre-specified series of tests automatically until either all the tests were completed or the participant showed inattention or

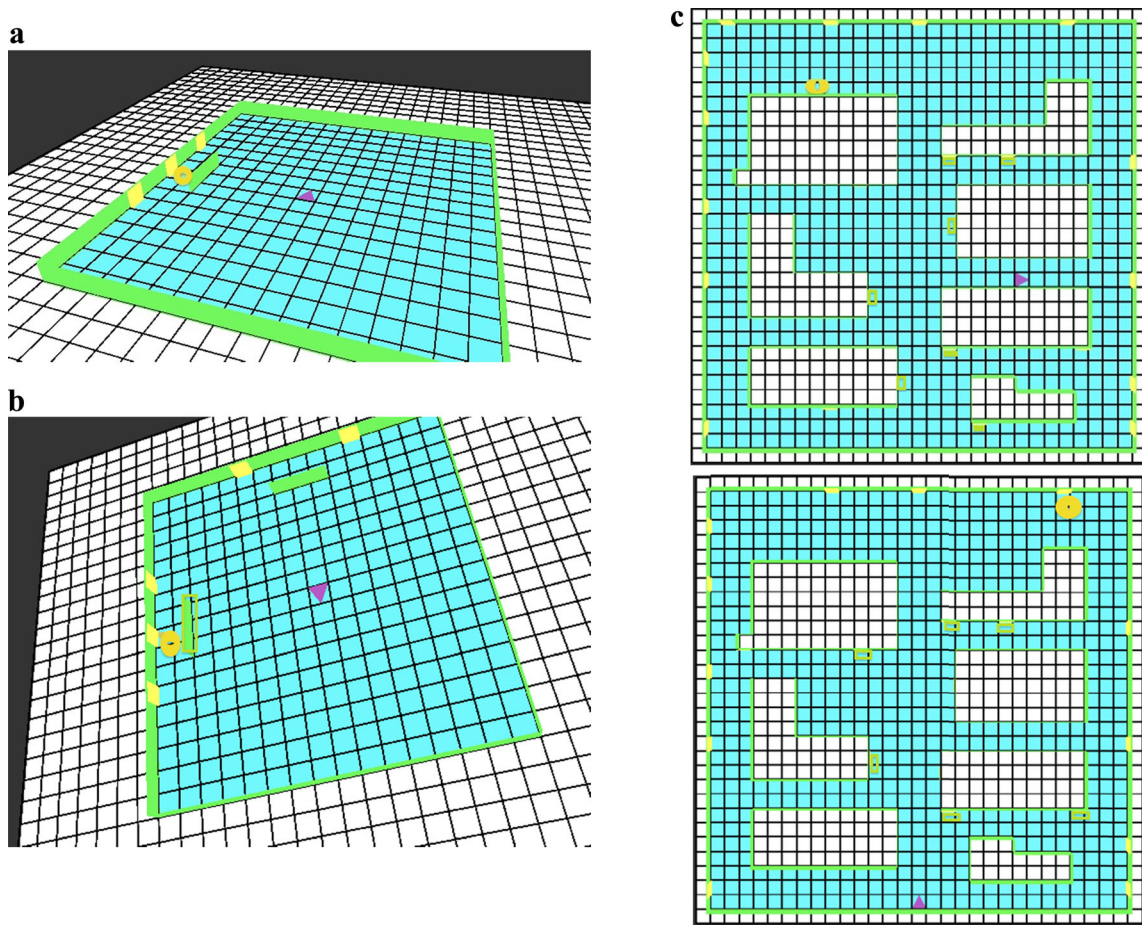


Fig. 4. This set of four diagrams present representations of the four types of VR open space designs used in testing; two of an open space test design presenting one or two 3D barriers located to occlude the view of the goal, and two presenting a complex (multi-alleyway) open space test design where the location of the start or goal is randomized per trial. In the barrier environments, two positive landmarks were placed either side of the barrier occluding the goal; in the design with two barriers, two negative landmarks were also paired with the other barrier. The barrier-landmark-goal array was set randomly, per trial, around the perimeter of the arena in one of four locations. In the complex open space designs, either the start position or the goal location was randomized over trials. In these complex designs, large visual barriers were constructed to create a complex set of alleyways. Positive/negative landmarks acted as guides to the location of the goal. The yellow squares symbolize the landmarks; the goal is represented by a yellow circle. The pink triangle symbolizes the start position and direction of view on beginning a trial. The green rectangles represent the barriers. (a) This figure represents an open space design of one barrier occluding the view of the goal. (b) This figure presents an open space design with two barriers occluding the view of the goal (yellow circle). Two positive landmarks (yellow squares) were paired with the barrier + goal (green rectangle and yellow circle) and two negative landmarks were paired with the other barrier. (c and d) These diagrammatic figures present two of the complex open space designs used in testing with the start position or the goal location randomized over trials.

frustration whereupon the testing session was terminated; the technicians tried to regain a subject's attention at a later time to complete the trials.

Data Analysis: Performance Evaluation in Virtual Environments (Optimal Path Analysis)

To address questions of performance of species and age groups in different types of environments and to evaluate degree of reliance on landmarks to localize the goal, the shortest path length possible was calculated using Euclidean distances taking into account barriers and alley structure from the start to goal location for each environment type, referred to as the "optimal path." For each participant trial

completed, the path length traversed in that environment was measured. This is referred to as the participants' "actual path length" or distance traveled.

Participants' "actual routes" were compared with that of a global information system (GIS) generated "optimal path" for each particular environment design, taking into account the placement of barriers. The GIS computation was done using ArcGIS, the ESRI program (www.ESRI.com, see details below), which allows for analysis and visualization of patterns within spatial data. The total length of the subject's route for each trial was determined by measuring within the ArcGIS application the sum total of distances between the test's output of X, Y data point coordinates. The subject's route distance

TABLE I. Numbers of Trials Completed Per Environment Type Per Individual

Species/ subject ID	Age (year)	Sex	Arena 8 random goal locations	Arena 1 barrier	Arena 2 barriers	Maze 1T	Maze 2T	Maze 3T	Complex maze
Chimpanzee									
Lana	37	F	51	23	**	34	4	**	1
Panzee	22	F	56	21	24	46	41	64	27
Mercury	21	M	151	60	59	40	44	64	**
Sherman	34	M	23	58	14	46	4	**	1
Human									
Jill 1	3	F	6	6	4	9	5	9	1
Jill 2	3	F	14	4	1	9	9	**	**
Jack 1	3	M	9	2	**	4	**	**	**
Jack 2	3	M	4	**	**	3	**	**	**
Jill 3	5	F	16	11	**	5	7	**	**
Jill 4	5	F	4	5	**	8	4	**	**
Jack 3	5	M	2	3	6	10	4	4	3
Jack 4	5	M	4	9	**	8	8	3	**
Jill 5	11	F	5	13	**	10	11	6	**
Jill 6	11	F	7	8	11	18	29	29	17
Jack 5	11	M	16	16	**	10	22	18	**
Jack 6	11	M	**	**	**	10	6	10	**
Juliet 1	48	F	16	14	10	10	16	20	12
Juliet 2	38	F	13	16	12	10	16	16	12
Romeo 1	43	M	16	16	12	10	25	38	22
Romeo 2	49	M	2	5	7	5	6	8	14

Units of measurement for travel are in *virtual* meters.

Subject did not participate in any trials in this environment type.

was then compared to the distance of the optimal path, that is, the shortest distance from the starting point to the goal site.

For purposes of comparison across participants a measure of travel efficiency (“shortest path ratio”) was calculated as the ratio of (length optimal path)/(length animal’s path) [Dolins, 2009; Menzel & Menzel, 2007; Menzel et al., 2002]. Units of measurement for travel are in virtual meters and do not correspond to actual distances in real space. Thus, the closer the ratio was to 1.0, the more proximal that trial performance was to optimal; the closer the ratio was to 0.0, the less optimal the trial performance.

Maps generated in the ArcGIS package, ArcView 9.1 (software produced by ESRI), overlaid the subject’s route data points with the given environmental design. These routes were examined pixel-by-pixel in the visual displays and geodatabase, relating all information to the maps, pixel-by-pixel (100 pixels per cell in a 35 × 35 cell design). These data were assigned to categories including decisions at choice points (defined as correct/incorrect), numbers of errors, latencies, touches/collisions onto objects in the virtual environments, and information about the virtual environment itself such as where landmarks were located in relation to choice points and distance from start to goal.

Determination of optimal routes is computationally non-trivial. Distance on a video screen is fundamentally non-Euclidean: cursor movement is

digital and discontinuous, and the shortest distance between two points is not always a straight line [Menzel & Menzel, 2007, p 183–188]. In the present task, translational movement along a 45° angle was not possible; virtual movement was “straight ahead” when the joystick was deflected forward, but circular rotation when the joystick was deflected L or R. Constraints on movement in the virtual environments were set within the VR software, with the aim of creating a task looked and felt reasonably natural and intuitive. The rules for movement were somewhat complex, and it was not practical to incorporate these rules into our computations of shortest possible paths. Thus, although we did take into account the locations of the start point, goal, and any visible barriers, we did not take into account some of the other software-generated constraints on movement that may have influenced the participants’ behavior and efficiency. For simplicity, we assumed a Euclidean metric and used the Pythagorean Theorem to estimate the shortest possible path lengths. For example, in the 1T maze, we used X–Y-coordinates to compute the Euclidean distances from the start point to the corner of the correct alley, and from the corner to the goal; the total distance served as our estimate for the shortest possible path. It is possible that the participants’ paths of movement would have appeared closer to the optimum, had we been able to take into account the additional constraints on movement. Nevertheless, if each step the individual moved reduced its remaining

distance to the goal by one step, with no backtracking, it would achieve a highly efficient “shortest path ratio” [Garber, 1989; Menzel & Menzel, 2007; Menzel et al., 2002, p 607–608].

Analysis

All analysis performed used a linear Mixed Model including a random intercept for subject to account for participant clustering. This method allowed us to include all corresponding trials per participant in the analyses. We chose this model because it accommodates uneven numbers of trials per individual. We also used various filters (described in the Results Section) to focus on environment types, participant groups and interactive effects. In our analysis, the Mixed Model makes a comparison of travel efficiency (shortest path ratio) based on type of participants (adult humans, teens, young children and chimpanzees). In particular, using either adult humans as the comparison group or the chimpanzees as the comparison group, the analysis determined how different the other participant types were from the comparison group based on shortest path ratio.

For each of the five participant groups (the chimpanzees, the 3 to 4, 5 to 6 and 11- to 12-year olds, and adults humans) there were an uneven number of trials completed. This was due to some individuals (particularly the younger children) choosing not to complete all trials in particular test environments: as environments became more complex, the younger children reported more difficulty and chose to end trials before localizing the goal or did not repeat trials more than once per environment (see Table I for a summary of the number of trials completed per subject and participant).

The results from the Mixed Model analyses presented are a mixture of the overall type III tests of fixed effects (F tests) and also the estimates of fixed effects (B coefficients from the model, thus t -test). All test results for overall effects are based on the model's type III tests of fixed effects and tests between specific levels of predictors based on model coefficients.

For all statistical tests, unless otherwise stated, the probability was $P < 0.001$. For tests that included all participants the degrees of freedom were 19; for the tests filtering out two of the chimpanzees, the degrees of freedom were 17; and for the tests filtering out three of the chimpanzees, the degrees of freedom were 16.

RESULTS

The chimpanzee and human participants successfully localized the goal in most of the environment types in which they were tested, with a few exceptions. Two exceptions were in the 3T-maze and complex (multi-alley) maze environments: only two (of the four) chimpanzees, two (of the eight) 3- to 6-year olds, while all four of the 11- to 12-year olds and

adult human participants were able to complete any trials in the 3T-maze and complex maze environments. Adult humans reported that these maze types were more difficult to navigate. Tables II–V present the compiled results of the chimpanzee and four human participant groups for all environment types.

The average shortest path ratio varied among species and age groups (Table III). Grouped by performance across all environment types, the chimpanzees' travel efficiency was similar to that of the 3- to 6-year-old children (3- to 4-year olds, $P = 0.059$; 5- to 6-year-olds, $P = 0.074$). The chimpanzees' average shortest path ratio was 0.324 while the 3 to 4-year-old children's ratio was 0.342. The average shortest path ratio combined for the 11 to 12-year-old children and the adult humans was 0.600. With the ratio closer to “1” as more optimal, it is clear that the 11- to 12-year-old and adult human participants outperformed the chimpanzees as a group ($P < 0.001$). Focusing only on Panzee, an adult female chimpanzee, her average shortest path ratio was 0.472, which was significantly different from the average shortest path ratio of the older humans (11- to 12-year olds and adults) combined, 0.504 ($P = 0.046$). However, Panzee's travel efficiency did not differ significantly from that of the younger children (3- to 4-year olds, $P = 0.711$ and 5- to 6-year olds, $P = 0.826$). The mean travel efficiency ratios were different between Panzee and the children, but the difference was not statistically significant. Examining the travel efficiency ratio for Panzee and the two younger groups of human participants averaged across all environment types (Table III), it is clear that Panzee outperformed them, using shorter distances to localize the goal position (Panzee's ratio = 0.472; 3- to 6-year-old children's ratio = 0.342).

There was a significant difference among participant groups in travel efficiency across the environment types ($P < 0.001$). Figure 5 represents participant group navigational efficiency ratio per environment type, displaying the relative level of accuracy (mean shortest path ratios). Per participant group, there was a decrease in the shortest path ratio as the complexity increased in mazes 1T–2T–3T. This indicates a decrease in travel efficiency and an increase in distance traveled, relative to the minimum possible distance, as the maze environments became more complex (complexity as defined by the number of choice points per environment and distance from start to goal). That is, the chimpanzees and human participants responded to the increasing degree of complexity with decreasing accuracy while simultaneously increasing distance traveled relative to the minimum possible distance.

The efficiency path ratio also varied by age and species, such that the younger children used longer paths to localize the goals than the other participant groups. This trend is apparent from the youngest children's (3- to 6-year olds) travel efficiency, which decreased most as the environments became more

TABLE II. Average of Actual Distance Traveled* for All Trials Per Environment Type Per Individual

Species/ subject ID	Age (year)	Sex	Arena 8 random goal locations	Arena 1 barrier	Arena 2 barriers	Maze 1T	Maze 2T	Maze 3T	Complex maze
Chimpanzee									
Lana	37	F	426.249	326.944	**	465.910	1363.592	**	915.170
Panzee	22	F	255.158	304.0528	285.744	277.588	704.241	706.231	933.518
Mercury	21	M	285.007	**	587.031	448.622	635.810	1028.810	**
Sherman	34	M	917.871	553.689	364.928	534.426	1791.138	**	523.279
Human									
Jill 1	3	F	214.469	194.147	251.885	215.205	386.505	723.682	1698.939
Jill 2	3	F	238.147	279.753	666.275	233.157	452.155	**	**
Jack 1	3	M	369.287	1027.903	**	473.033	**	**	**
Jack 2	3	M	307.254	**	**	209.343	**	**	**
Jill 3	5	F	314.680	321.243	**	254.998	586.554	**	**
Jill 4	5	F	139.158	149.453	**	204.196	496.200	**	**
Jack 3	5	M	192.912	262.262	252.740	193.372	486.989	635.636	920.812
Jack 4	5	M	249.152	193.904	**	195.505	307.847	460.504	**
Jill 5	11	F	137.325	159.669	**	192.557	360.868	461.230	**
Jill 6	11	F	113.473	116.926	127.302	164.947	296.137	330.122	733.086
Jack 5	11	M	111.402	132.477	**	170.706	325.071	378.255	**
Jack 6	11	M	**	**	**	183.552	351.080	368.430	**
Juliet 1	48	F	127.737	160.572	151.278	190.511	297.086	295.354	536.367
Juliet 2	38	F	252.930	248.625	221.804	181.296	355.972	456.776	667.773
Romeo 1	43	M	110.391	151.157	115.375	189.009	302.223	350.150	529.777
Romeo 2	49	M	162.324	106.017	104.066	168.344	299.854	288.036	366.253

*Units of measurement for travel are in *virtual* meters.

**Subject did not participate in any trials in this environment type.

complex (Fig. 5, and also Tables III and IV). Thus, in general, across all participant groups regardless of species, as the level of environmental difficulty increased, the level of navigational efficiency decreased. Younger children showed more marked effects with increasing maze complexity related to decreased travel efficiency.

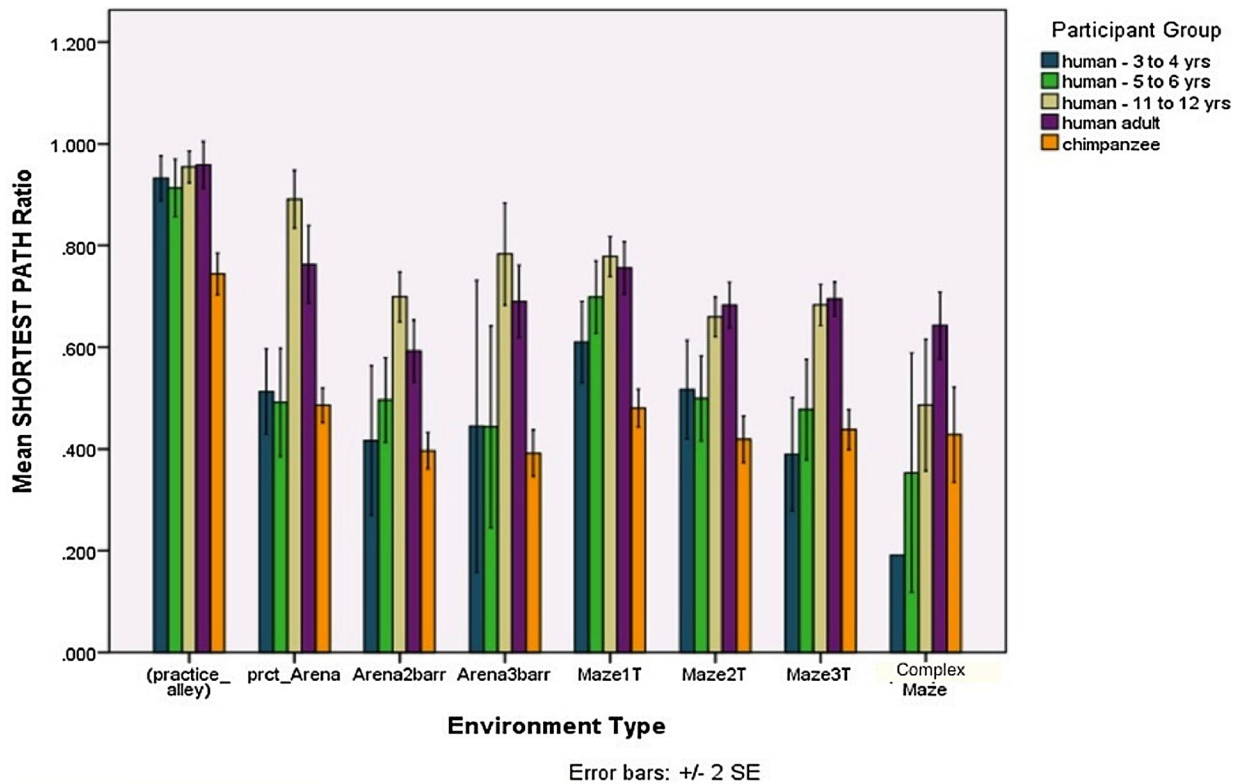
As indicated in Figure 5, of all the participant groups the 11- to 12-year olds' travel employed the shortest paths, followed by that of the human adults. There was a difference in average performance of the chimpanzees from that of the 11- to 12-year olds and adult human participant groups for all environment types presented (with exceptions in the 3T and complex mazes), favoring the human's performance as more efficient ($P < 0.001$). As a group, the chimpanzees displayed less travel efficiency and

greater distance traveled than the older children and adult human counterparts (this differed by individual chimpanzees, as discussed further on). However, as a group, the chimpanzees' shortest path ratio is comparable with the 3- to 4-year olds and 5- to 6-year olds (3- to 4-year olds, $P = 0.059$ and 5- to 6-year olds, $P = 0.074$).

There were no significant differences in participant group performance in travel efficiency in the 3T-maze ($P = 0.122$). There were, however, significant differences in travel efficiency in the remaining environments ($P < 0.001$). This travel efficiency favored the chimpanzees when comparing them directly to the younger children (Tables IV and V), particularly in the more complex maze environments. It should be noted, however, that only one of the 3- to 4-year olds and only one 5- to 6-year olds completed

TABLE III. Average Optimal/Actual Path Ratio (Travel Efficiency*) for Panzee, All Chimpanzees, Children, and All Human Participants Combined Per Environment Type

Participant	Arena 8 random goal locations	Arena 1 barrier	Arena 2 barriers	Maze 1T	Maze 2T	Maze 3T	Complex maze	Average shortest path ratio across all environments
Panzee	0.540	0.413	0.422	0.623	0.463	0.396	0.445	0.472
All chimpanzees	0.440	0.259	0.274	0.477	0.313	0.186	0.320	0.324
Children (3–6 years)	0.560	0.417	0.141	0.660	0.375	0.172	0.069	0.342
Adults (11–12 years + adults)	0.707	0.574	0.440	0.774	0.653	0.671	0.381	0.600
All humans combined	0.634	0.469	0.547	0.717	0.514	0.421	0.225	0.504



Environment Type Code
prct_Arena = open space Arena with 1 of 8 random locations per trial for the goal
Arena1barrier = open space Arena with and goal hidden behind a barrier, two positive goals on either side.
Arena2barrier = open space Arena with and goal hidden behind one of two barriers; barrier with the goal has two positive goals on either side.
Maze1T = 1T-maze with one junction/decision point.
Maze2T = 2T-maze with two junctions/decision points; randomized location for goal.
Maze3T = 3T-maze with three junctions/decision points; randomized location for goal.
Complex Maze = maze with multiple junctions/decision points (more than 4); randomized goal or start location.

Fig. 5. Mean shortest path ratio per participant group in different environment types.

one complex maze trial, whereas two of the chimpanzees completed multiple trials of this environment type. As a result, it is difficult to make comparisons between the younger children and the two chimpanzees who showed relatively few signs of difficulty navigating in these more complex environments.

As described above, in our analyses we initially compared all trials in all environments using the shortest path ratio as the dependent variable. The four chimpanzees were the reference group for comparison to that of the 3 to 4, 5 to 6, and 11 to 12-year-old children and human adults. And, for each of the five participant groups (chimpanzees, the 3 to 4,

TABLE IV. All Trials Optimal/Actual Path Ratio Averaged (Travel Efficiency*) Per Individual Per Environment Type

Species/ subject ID	Age (year)	Sex	Arena 8 random goal locations	Arena 1 barrier	Arena 2 barriers	Maze 1T	Maze 2T	Maze 3T	Complex maze
Chimpanzee									
Lana	37	F	0.396	0.337	**	0.437	0.190	**	0.304
Panzee	22	F	0.540	0.413	0.422	0.623	0.463	0.396	0.445
Mercury	21	M	0.473	**	0.323	0.489	0.440	0.346	**
Sherman	34	M	0.350	0.286	0.349	0.357	0.159	**	0.532
Human									
Jill 1	3	F	0.527	0.546	0.560	0.659	0.531	0.393	0.193
Jill 2	3	F	0.531	0.359	0.130	0.613	0.517	**	**
Jack 1	3	M	0.511	0.090	**	0.511	**	**	**
Jack 2	3	M	0.568	**	**	0.707	**	**	**
Jill 3	5	F	0.391	0.432	**	0.617	0.394	**	**
Jill 4	5	F	0.838	0.617	**	0.715	0.413	**	**
Jack 3	5	M	0.605	0.340	0.439	0.741	0.499	0.419	0.357
Jack 4	5	M	0.511	0.532	**	0.718	0.644	0.563	**
Jill 5	11	F	0.833	0.630	**	0.726	0.592	0.544	**
Jill 6	11	F	0.933	0.771	0.768	0.819	0.683	0.705	0.485
Jack 5	11	M	0.908	0.695	**	0.797	0.645	0.672	**
Jack 6	11	M	**	**	**	0.776	0.586	0.655	**
Juliet 1	48	F	0.814	0.600	0.649	0.768	0.712	0.778	0.622
Juliet 2	38	F	0.492	0.420	0.459	0.755	0.620	0.531	0.505
Romeo 1	43	M	0.904	0.644	0.798	0.739	0.702	0.694	0.600
Romeo 2	49	M	0.771	0.834	0.848	0.814	0.687	0.786	0.839

*Units of measurement for travel are in *virtual* meters.

**Subject did not participate in any trials in this environment type.

TABLE V. Average of Initial Three Trials of Optimal/Actual Path Ratio (Travel Efficiency*) Per Individual Per Environment Type

Species/ subject ID	Age (year)	Sex	Arena 8 random goal locations	Arena 1 barrier	Arena 2 barriers	Maze 1T	Maze 2T	Maze 3T	Complex maze
Chimpanzee									
Lana	37	F	0.518	0.399	**	0.616	0.190	**	0.304
Panzee	22	F	0.743	0.526	0.536	0.815	0.657	0.535	0.548
Mercury	21	M	0.555	**	0.465	0.746	0.699	0.531	**
Sherman	34	M	0.410	0.462	0.456	0.598	0.159	**	0.532
Human									
Jill 1	3	F	0.52729	0.546	0.560	0.643	0.531	0.430	0.195
Jill 2	3	F	0.521	0.359	0.130	0.572	0.517	**	**
Jack 1	3	M	0.511	0.090	**	0.511	**	**	**
Jack 2	3	M	0.568	**	**	0.707	**	**	**
Jill 3	5	F	0.391	0.447	**	0.654	0.430	**	**
Jill 4	5	F	0.838	0.617	**	0.713	0.413	**	**
Jack 3	5	M	0.605	0.340	0.439	0.727	0.499	0.419	0.357
Jack 4	5	M	0.511	0.532	**	0.702	0.644	0.563	**
Jill 5	11	F	0.833	0.654	**	0.723	0.608	0.544	**
Jill 6	11	F	0.932	0.771	0.768	0.808	0.683	0.708	0.442
Jack 5	11	M	0.908	0.694	**	0.817	0.647	0.694	**
Jack 6	11	M	**	**	**	0.761	0.586	0.637	**
Juliet 1	48	F	0.814	0.643	0.649	0.674	0.679	0.779	0.600
Juliet 2	38	F	0.492	0.407	0.459	0.784	0.620	0.527	0.486
Romeo 1	43	M	0.904	0.628	0.798	0.767	0.664	0.690	0.604
Romeo 2	49	M	0.771	0.834	0.848	0.814	0.687	0.786	0.784

*Units of measurement for travel are in *virtual* meters.

**Subject did not participate in any trials in this environment type.

5 to 6, and 11- to 12-year olds, and adult humans) there were an uneven number of trials completed. In order to better examine possible group and individual differences, we filtered out two of the chimpanzees' data to focus on Panzee and Mercury, whose performance and apparent enthusiasm for this virtual spatial task was greater than that of the other two chimpanzees, Lana and Sherman. We also reduced the human participants to two groups, "children" (3 to 4 and 5 to 6-year olds) and "adults" (11 to 12-year olds and adult humans) based on the similarity in performance of the two younger groups of children and the similarity of the older children to that of the adults.

Still using a Mixed Model analysis, we compared Panzee and Mercury as the reference group to that of the children and adults using the shortest path ratio as the dependent variable. Summing across environment types, the analysis indicated that the children were not significantly different in travel efficiency from Panzee and Mercury on measures of shortest path length ($P = 0.535$). However, there was a significant difference between the chimpanzees' and adult humans' performance ($P < 0.001$), favoring the adults. Specifically, the average shortest path ratio for all human trials was 0.504 and the average shortest path ratio for Panzee and Mercury was 0.448 (the closer the ratio is to 1, the more optimal).

It is worth noting (Table I) that the average shortest path ratio for all of Panzee's trials in all environments is 0.472, the average shortest path ratio for Panzee and Mercury is 0.384 and for all four chimpanzees the average shortest path ratio is 0.324, while the average shortest path ratio for all trials for all humans is 0.504, and for just the younger children (3 to 4 and 5 to 6-year olds) is 0.342 (with shortest path ratios closer to "1" more optimal). When comparing Panzee and Mercury it is clear that these chimpanzees' shortest path ratios are highly similar to those of the younger children.

We filtered out three of the chimpanzees' data to focus on Panzee's data set alone. She was observed to perform the virtual spatial tasks with greater accuracy than that of the other chimpanzees. Thus, with Panzee's data set as the reference group, summing across environment type and using the shortest path ratio as the dependent variable, we compared all of her trials to that of the younger children and to the 11- to 12-year olds and human adults. The analysis showed a significant difference in performance between Panzee and the adult humans and the 11- to 12-year-old children (adults: $P = 0.046$; 11- to 12-year olds: $P = 0.043$). However, when examining Panzee compared to the two younger groups of children (3 to 4 and 5- to 6-year olds), these three groups clearly showed no significant difference from each other in performance based on shortest path ratio (3- to 4-year olds: $P = 0.729$; 5- to 6-year olds: $P = 0.839$).

Across environment type, the comparison of Panzee's trials to that of all four human participant groups combined revealed significant differences in performance with the adults and 11- to 12-year olds (adult humans compared to Panzee, $P = 0.047$; 11- to 12-year olds, $P = 0.044$) with one exception. The exception was the one-barrier open space in which there was no significant difference ($P = 0.083$). This environment type is a large, open square with one barrier wall and positive landmarks demarcating the location of the hidden goal behind the barrier. The comparison of Panzee's trials to that of the two groups of younger children revealed no significant differences in performance (3- to 4-year-old children compared with Panzee, $P = 0.711$; 5- to 6-year olds, $P = 0.826$). Moreover, it is notable that the difference between Panzee's shortest path length and that of the younger children favors Panzee; she clearly uses shorter distances to localize the goal (see Table II for comparisons of travel efficiency per participant in different environment types).

A similar pattern of comparisons of Panzee's data set compared as the reference group to the two reduced human participant groups, children (3- to 6-year olds) and adults (11- to 12-year olds + adults), revealed that the humans' performance were not significantly different from that of Panzee (children: $P = 0.197$; adults: $P = 0.087$). In fact, it favored the chimpanzee's performance compared to that of the children. According to the shortest path ratios, Panzee outperformed the children on travel efficiency over all environment types (Table IV). The average shortest path ratio (across environments) for the children was 0.342 and for the adults was 0.600 compared to that of Panzee's average, which was 0.472 (with "1" being closer to optimal).

An examination of Panzee's five best trials in all environment types provides an interesting picture when comparing her performance to the human participant groups because five is the highest number of trials that most of the human participants completed across environment types. In this analysis, also using the Mixed Model, the shortest path ratio was applied as the dependent variable in comparing Panzee's five best trials to that of the four human participant groups. Across environment type, it is notable that there was no significant difference between Panzee's performance on travel efficiency and that of the four human participant groups (3- to 4-year olds: $P = 0.362$; 5- to 6-year olds: $P = 0.361$; 11- to 12-year olds: $P = 0.356$; and adults: $P = 0.328$). However, focusing only on Panzee's data compared to the two reduced human groups, children and adults, we used *only* the data from her trials in the two most complex environments, the 3T-maze and the complex maze. We compared these data to the two reduced human participant groups' ("children" and "adults") travel efficiency in *all* environments based on the shortest path ratio.

This analysis then focuses on Panzee's data (efficiency ratios) from her performance in the two most challenging, complex environments compared to humans' performance in *all* the environment types, including some of the less complex environments (e.g., the 1T-maze).

Overall, the results indicate that Panzee's travel efficiency was not significantly different from that of the children or the adults' performance ("children": $P=0.229$; "adults": $P=0.092$). Travel efficiency among the two reduced human groups and Panzee in the most complex environments showed no significant differences in the 2T-maze ($P=0.477$), 3T-maze ($P=0.660$), and one-barrier ($P=0.845$) and two-barrier environments ($P=0.919$). This suggests that the three groups were not performing significantly differently from each other in these environments.

In the straight alleyway environment (training) there is no significant difference in performance between the "children" and Panzee ($P=0.308$) and only a significant difference in performance between the "adults" and Panzee ($P=.043$). However, there was a significant difference in performance between the two human groups and Panzee in the 1T-maze environment ($P < 0.001$).

Highly notable is the significant difference in performance in the complex maze environment ($P < 0.001$), which favors Panzee's travel efficiency. It is striking that Panzee significantly outperformed all the human participants in the complex maze environments: Panzee's average shortest path ratio was 0.445, while averaging all the human participant's performance was 0.225 and specifically that of the 11- to 12-year-old children and adults was 0.381. Thus, examining the average shortest path ratios of all human participants and Panzee comparatively (Table III), it is clear that in the complex maze environments Panzee performed with higher accuracy than her human counterparts. Note that in the complex mazes, the younger children did not complete many, or in some cases, any of these trials, thus the main comparisons are between Panzee's data and the adult humans (11- to 12-year olds and the adults).

Table V presents results of the shortest path ratio for all participants' first three trials. It is worth noting the results for Panzee in comparison with the one 3-year-old (female) who attempted (but did not complete) the complex maze (1 trial) and the adults. The complex maze environment was designed so that it would be very difficult to identify the location of the goal without close attention to the type of landmark that provided directional information. Attention to the positive and negative landmarks, therefore, was essential to localizing the goal in an efficient manner. Therefore, indirectly, these results suggest that Panzee, in comparison with the younger and older children, was able to closely attend to the landmarks

in order to localize the goal in this complex maze environment. Panzee's average path length ratio from the first three trials in the complex maze environment (0.548) was comparable to the average for the four human adults' first three trials (0.600, 0.486, 0.604, and 0.784) and suggests that she was within an adult human range for travel efficiency (Table V). By comparison, the one 11-year-old female who completed any trials in the complex maze environment, had an average ratio of 0.442 for her first three trials. Thus, Panzee's performance showed greater travel efficiency.

In all three of the more complex environments (2T, 3T and complex maze), Panzee displayed the ability to navigate where some of the younger children could not. Moreover, in the complex environments (3T-maze and complex maze), Panzee's performance was not significantly different from that of the adults ($P=0.660$).

Additionally, across environment types when examining distance traveled, there was no significant difference between participant groups ($P < 0.001$). From the average distances traveled in each environment per participant, it is clear that Panzee navigated paths of a shorter distance than some of her human counterparts. For example, the average of the three initial trials in the 3T-maze and complex maze, Panzee's distances traveled were 466.008 and 898.431 virtual distance units, respectively. For Jill 3 (a 5-year-old girl), her distances traveled in the same environments on the same trials were 635.636 and 920.812; for Jill 5 (11-year-old female), her distances traveled were 642.988 and 1698.939; and finally for Juliet 1 (adult female), her distances traveled were 295.968 and 550.115, respectively. It is apparent that in terms of travel distances in the most complex environments, Panzee outperformed both the 3- and 11-year-old girls but not, for example, Jack 6 (11-year-old boy), whose distances traveled of 324.802 and 782.119 in the 3T-maze and complex maze, respectively, were slightly better than Panzee's initial three trials.

DISCUSSION

This study sought to investigate the comparative performance and spatial cognitive abilities of four captive chimpanzees, 12 children and four adult humans, navigating in increasingly complex virtual environments. Our goal was to determine how chimpanzees' performance compared to that of humans on a number of variables. These variables included determining measures of travel efficiency, distance traveled, performance in increasingly complex environments, and indirectly, attention to landmarks as guides to localize the goal and quality of decision-making at choice-points. In this way we aimed to ascertain whether virtual reality was a

viable mode of testing chimpanzee spatial cognitive abilities.

Our results suggest that both the humans and chimpanzees learned to discriminate between the positive and negative landmarks in the virtual environments to successfully localize goal sites [cf. Garber & Dolins, 1996]. Notably, we observed differences in performance by species, age, and complexity of environment: young children compared to adult chimpanzees, adult humans and the older children, deviated from an optimal route more extensively when navigating in more complex mazes (e.g., 2T-maze compared to the 1T-maze; two-barrier to one-barrier environments). This suggested a comparative lack of attention by young children to directional cues (e.g., turning at choice points regardless of landmark information) and secondarily to landmarks to re-establish correct directional information to localize the goal. Similarly, compared to the other three participant groups, the youngest children showed less efficiency in distinguishing correct paths as maze complexity and environment size increased.

In terms of travel efficiency, there was an effect of age and complexity of environment on travel efficiency, that is, on shortest path ratios. Thus the younger children clearly had more difficulty (and reported this during and after testing sessions) in completing trials in the more complex environments. Older children and adults did not show or report this same difficulty except for the complex maze environment, which all reported as being “challenging” and “difficult.” To this end, it is clearly notable that Panzee performed so well in the most complex environments.

Comparing performance between environment types, there was a decrease in the ratio score, as expected, across Maze 1T–2T–3T; this suggests that the task succeeded in scaling the difficulty of the task in some fashion. We assume that the increasing number of turns (and lack of visibility of the goal until the last turn) was a key factor here, but of course the increased total distance also gave the participants more opportunities to make an incorrect move with the joystick and to become confused or disoriented.

In order for participants to have shown high travel efficiency in any of the environments, they presumably needed to attend to the positive and negative cues provided. The experimental design purposely randomly shifted the location of the goal in each environment type so that participants could not use fixed movement patterns to localize the goal efficiently. Accordingly, landmarks shifted to highlight the correct/incorrect paths. It was impressive to the observers to note that on initially testing Panzee in the 1T-maze environment test runs, on her second trial in the 1T-maze (in which the goal shifted from the left of the T-junction to the right), she made one initial error in turning to the left first. Upon seeing the negative landmark, turned abruptly 180° around and headed to the right arm of the T-maze; thereafter

she made no errors on the 1T-mazes. It was clear that she was attending to and discriminating between the type of landmarks in order to localize the goal with maximum travel efficiency. The two youngest groups of children, by contrast, were observed to perform with greater inaccuracy on a number of trials on the 1T-mazes before they began to attend more carefully to the landmarks. In the older group of children and adults, some reported that while navigating they were looking at the landmarks provided for directional information.

It is interesting to note that Panzee had the second best ratio score of all participants on her first three trials of Maze 1T. Visual examinations of the paths taken by each of the participants reveals that she was more apt than the humans to cut close to the corners rather than “square off” turns at corners in all environments, and that this saved her some distance and enhanced her shortest path ratio.

While older humans demonstrated the most efficient navigation paths overall, the adults and children showed underperformance compared to Panzee in the set of most complex mazes presented. Our findings suggest that chimpanzees and humans learn and respond to virtual environments similarly, discriminating between landmarks to enhance navigational decisions in adapting to challenges of environmental complexity. However, age differences occur in the human data set. The youngest children not only had the highest measures of path length among the three human participant age groups but compared to the chimpanzees the children’s path length was also greater in each environment. Unfortunately, it is not possible to test young chimpanzees at an equivalent stage in development on the same tasks to determine age-related and developmentally related effects on performance in each species. To date, studies of spatial cognitive development in young chimpanzees are scarce, so comparative data are not available about how chimpanzee spatial strategies and attention to landmarks develop through infancy and juvenile stages.

Focusing on different strategies employed by participants in localizing the goal in different maze types provides some insight into how those individuals perceive those environments for navigation. For example, in the “arena” environment that had an open, square space with eight random goal locations, two main navigational strategies emerged. This environment, a large, square space where the participant found themselves on each new trial, facing north, also had the goal (not hidden) located in one of eight locations: either on one of the four walls or on one of the four corners. If the goal was not directly in front of the participant at the start of a trial (the goal location was randomized per trial), then the most effective strategy (shortest path) would be to turn in place until seeing the goal and then, in a

straight line, travel to it. A less effective, but still efficient strategy, would be to head directly to the wall and follow the perimeter of the wall until hitting into the goal. This could be a shorter distance if the goal happened to be closer to the direction of turning, or farther away. So as a strategy, it has a 50/50 chance of being efficient. However, in using this type of strategy, the participant also may learn additional information about that space, such as the distance between corners, or the distance between the start position and walls and corners (which, in this environment, remained equidistant). A third strategy was possible, but interestingly was never used by any of the participants, chimpanzee or human. This would have been to randomly or pseudo-randomly move about the space between the start position and the walls and corners until hitting into the goal. The estimation is that random movement of this type would have been the least efficient in terms of shortest path length, although as none of the participants employed this strategy, this cannot be tested.

What was fascinating about the strategies employed in this arena with eight random locations, is that both the humans and the chimpanzees used a strategy on the first trial, and continued with it until the trials ended. Moreover, use of a strategy was not species or age specific. Panzee employed the most efficient strategy of turning in place until seeing the goal and then heading towards it. Of the humans, two of the adults and some of the older children did the same, but most adopted the strategy of heading directly to the wall and then following the perimeter until reaching the goal. Overall, approximately 80% of the participants, chimpanzee and human, used the "wall hugging" method, while only one chimpanzee (Panzee) and three humans used the alternative, more efficient strategy.

Similarly, navigation patterns in the two types of barrier environments (large, square space with the goal hidden behind a barrier associated with positive landmarks or behind one of two barriers, one associated with positive landmarks), revealed two major strategies: the most efficient would be, at the start of each trial, to stay, turn in place at the start position until identifying the location of the goal, and then navigate in a straight line toward it. A less efficient strategy would be to begin traveling (in any direction), and then identifying the location of the goal, travel in a straight line toward it. Of interest in the navigation patterns in these two barrier environments compared with the arena (eight random locations of goal) environment was the strategy adopted by even those participants who were previously highly efficient navigators, and the different strategies employed between the one barrier environment versus the two barrier environment. Most of participants who elected a most efficient strategy in the arena environment also used that

strategy in the one barrier environment. Use of the most efficient strategy in the one barrier environment included all four chimpanzees, the 11- to 12-year olds and the adults, but only a few of the 3 to 4 and 5 to 6-year-old children. However, a notable shift toward employing the less efficient strategy occurred when the two barrier environment was introduced; interestingly, this new strategy once adopted, was not altered during the course of the trials. All participants began traveling prior to looking for the positive landmarks associated with the barrier obscuring the goal, adjusting their direction of travel as they observed either the absence of the landmarks or their presence. They did not adjust their strategy over trials in the two-barrier environment. However, it is interesting to note that the individuals (including Panzee) who used the most efficient strategy in the arena and one-barrier environments, still produced the shortest paths to the goal. Observations of their paths reveals that although they began traveling prior to noting the position of the goal, they quickly adjusted their direction of travel, compared to the other participants who traveled farther and then adjusted direction of travel towards the goal.

From trials in these three environment types, it is clear that both species, regardless of age, altered their strategy across environments. In principle, participants could have applied the same, most efficient strategy in all three environments, that is, stay in place, turn until identifying goal position and then travel in a straight line to it. What was different in these environment types was whether the goal was hidden, and how many barriers existed and so required a choice or discrimination between two clear alternatives (i.e., barrier associated with positive landmarks or barrier with no landmarks).

Of note is that with increasing complexity in these open space environment types, the increase in spatial information (i.e., the addition of barriers and positive and negative landmarks) led to a decreased efficiency of strategy. This parallels the trends in travel efficiency as the maze environments increased in complexity. However, the difference between the maze and arena/open space environments is one of overview. According to Poucet [1993], the maze environments would be considered as large-scale space in not providing an overview of the landmarks and goal, while the arena/open space environments would be considered as small-scale space in providing the opportunity for an overview if that strategy was implemented. What is fascinating, is that predictions from Poucet's distinctions between small- and large-scale space, of greater accuracy in small-scale space was supported but only when less spatial information was available (i.e., only when no barriers or positive and negative landmarks were present). As this increased, efficiency of travel decreased. Similarly too, in large-scale space, Poucet's prediction of less

accuracy is supported but even more so, as the large-scale environments become more complex.

In summary, in assessing nonhuman primates' spatial strategies in their natural habitat, the difficulty lies in being able to determine what salient visuo-spatial landmarks are being attended to and how the animal perceives and represents a particular environment. VR creates an experimental situation where both some degree of ecological validity and control over variables are afforded while simultaneously presenting environments that vary in features, scale, and complexity. This paper presents a novel methodological approach to address issues of integration of visuo-spatial information in internal representations and spatial strategies of nonhuman primates. The results of this study support the use of VR as a method for investigating spatial cognitive abilities of captive nonhuman primates. The data indicate that the chimpanzees were on par with younger children's performance and, to some degree, had comparable performance to that of the older human participants. The chimpanzees' spatial behavior in localizing a goal site is not qualitatively different from that of the human participants. Indirectly, the comparable navigational performance of the chimpanzees in VR environments suggests a perception of the two-dimensional virtual simulations as some kind of space within which to move, travel and navigate.

The use of VR provides fascinating avenues for further research on how apes, and other animal species, perceive their world and by what cognitive mechanisms they interpret perceptual details to problem-solve successfully. While we were not testing chimpanzee spatial memory per se, it clearly would be possible to use VR to model real environments with foraging/goal sites of varying amounts and types of food [cf. Janmaat et al., 2013; Normand et al., 2009; Sayers & Menzel, 2012]. In this way, assessments of routes, efficiency of travel, temporal as well as spatial elements can be configured and measured via virtually realistic environments. Data can be evaluated on which visual elements chimpanzees might be focusing while traveling at any given point in time.

VR inherently allows for flexibility in presenting variables such as scale and complexity of simulated environments, landmark type, quantity, and location of landmarks, as well as the choice of constructed or naturalistic simulations that also, in principle, could engage the auditory system via embedded sounds. It provides the opportunity to test attention to, and use of, visuo-spatial information incorporated into spatial strategies, to test equivalent spatial problem solving across species without need for language, and to solve real-life problems that otherwise would be difficult or impossible to test in the laboratory: comparing small- and large-scale space and levels of complexity in spatial cognitive research becomes achievable. Thus, VR uniquely affords insight into

the cognitive, developmental, and evolutionary origins of adaptive behaviors in nonhuman and human primates.

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