APPLIED ECOLOGY

Chimpanzees (*Pan troglodytes*) navigate to find hidden fruit in a virtual environment

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Almost all animals navigate their environment to find food, shelter, and mates. Spatial cognition of nonhuman primates in large-scale environments is notoriously difficult to study. Field research is ecologically valid, but controlling confounding variables can be difficult. Captive research enables experimental control, but space restrictions can limit generalizability. Virtual reality technology combines the best of both worlds by creating large-scale, controllable environments. We presented six chimpanzees with a seminaturalistic virtual environment, using a custom touch screen application. The chimpanzees exhibited signature behaviors reminiscent of real-life navigation: They learned to approach a landmark associated with the presence of fruit, improving efficiency over time; they located this landmark from novel starting locations and approached a different landmark when necessary. We conclude that virtual environments can allow for standardized testing with higher ecological validity than traditional tests in captivity and harbor great potential to contribute to longstanding questions in primate navigation, e.g., the use of landmarks, Euclidean maps, or spatial frames of reference.

INTRODUCTION

Almost all animals navigate within their environment to achieve goals of finding food, shelter, and mates (*1*, *2*). Species-specific selection pressures have equipped animals with a range of navigation skills attuned to their specific requirements, including homing (*3*), migration (*4*), and exploiting spatiotemporal patterns of food distribution (*5*–*10*). A consequence is that spatial cognition—broadly defined here as spatial perception, memory, short-term decision-making, and planning in the service of navigation—reflects adaptations to these pressures at all levels of psychological description. This includes the neurophysiological implementation (*11*, *12*); the representational format, e.g., topological versus Euclidean map use (*10*, *13*); and the evolved function, e.g., a more frugivorous, as opposed to a more folivorous, diet has been hypothesized to select for faster rates of learning, retention of greater numbers of locations of preferred foods, and longer retention rates (*9*, *14*). Describing at these different levels how species use spatial cognition informs not only theories of the evolution of intelligence but also conservation, e.g., rewilding efforts, modeling animal home ranges (*15*–*17*), and the reverse engineering of spatial cognitive processes for robotics (*18*).

Primate spatial cognition has been studied in two separate disciplines, behavioral ecology and experimental primate cognition. Researchers who observe primate behavior in the wild investigate what strategies primates use to exploit the spatial and temporal variation in the availability, distribution, and productivity of resources in their environment in an efficient, reliable, and safe way. There have been substantial advances in recent years, enabled by new technology used for recording primate movement data, such as drones, thermal cameras, and GPS tracking (*19*–*21*), as well as the development of statistical and modeling tools for analyzing movement data to reveal signatures of cognitive processes (*13*, *22*–*25*). Questions concern how and why travel paths become "routes" (*26*–*28*) and what travel efficiency reveals about an individual's motivations, their memory, and the nature of their cognitive map (*7*, *10*, *29*, *30*). Other questions concern how travel decisions are formed and specifically how ecological variables such as annual and seasonal patterns of resource availability (*31*), clustering of resources (*9*, *13*), and inter- and intraspecies competition over the same resources (*32*, *33*) influence these decisions. Field researchers often go to great lengths to assess site-specific variables and rule out confounds through meticulous observation and measurements or manipulation of the environment and the socioecological context (*23*, *33*–*36*). Field studies provide an accurate perspective on how parts of a species' behavior system fit into its broader life history pattern. Field studies help us discover the types of problems animals face and solve in their natural habitat and can direct us to the evolutionary and developmental challenges that shape a species' cognitive abilities. However, one problem that remains is that clear and comprehensive data collection in the field can be time-consuming, and knowledge about past experiences of wild animals is limited.

Advances have also been made in assessing spatial cognition with captive primates in more restricted and physically controlled experimental environments. Researchers in this tradition study the representational format of spatial cognition. They aim to identify what units of information and algorithms are used by primate brains when cognitive maps are generated, updated, and accessed to guide behavior (*37*). Primates in captive studies are often given an experimental manipulation (e.g., preexposure to an enclosure or stimulus array), followed by a test, such as foraging in the enclosure or manually choosing an item (*38*–*40*). Questions range from the study of path efficiency (*38*, *41*), egocentric versus allocentric frame

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of reference (*39*, *42*), attention to and use of landmarks and environmental features, memory for food locations after minimal exposure (*5*, *40*, *43*), to the relationship between a species' feeding ecology and their performance in small-scale spatial memory tests (*14*, *44*). In addition, some studies have tested navigation in different primate species in simulated joystick-controlled two-dimensional (2D) maze tasks (*45*–*47*) and barrier-and-detour tasks (*48*), providing subjects with a problem overview analogous to a pencil-and-paper maze. However, here, the problem that remains is that, compared to field settings, captive environments often considerably limit the physical scale at which problems can be presented to subjects, which may affect motivation, locomotion, decision-making, working memory load, and other aspects in ways that can challenge generalization to real-life navigation (*49*).

Virtual environments may solve both problems by allowing for simulated wide, open spaces with navigational flexibility in combination with rigorous control over the presentation of stimuli and recording of responses. Studies of human navigation have integrated 3D virtual environments for almost 30 years (*50*–*54*). In the study of nonhuman primate navigation, the introduction of 3D virtual environments is much more recent. Neurophysiological studies have investigated rhesus macaque (*Macaca mulatta*) navigation via a joystick in simple 3D mazes to study how they find their way to familiar goals from novel starting points (*55*), how eye movement compares between virtual foraging and traditional methods (*56*), and how hippocampal cells contextually code virtual landmarks (*12*, *57*). To date, only three virtual studies have worked noninvasively and without head fixation, those by Washburn and Astur (*58*) and by Dolins *et al.* (*49*, *59*). Washburn and Astur (*58*) first trained four macaques to navigate from a consistent starting point to a goal object that was located somewhere in a simple 3D cross maze. This task progressed gradually from seemingly easy conditions with the goal object in plain sight to more and more difficult ones that required reorienting at multiple intersections. The monkeys succeeded eventually, albeit after considerable amounts of training and testing (on average, more than 3500 trials). Dolins *et al.* (*49*) trained between one and four chimpanzees to navigate virtual alley mazes with one, two, or three choice points and an "open-space maze" with none, one, or two barriers along the walls that hid potential goal locations. Navigation was aided by one of two associative landmarks that signaled where the goal was located. All chimpanzees succeeded on the T-mazes with two choice points, and two chimpanzees succeeded eventually on T-mazes with three choice points. Path efficiency (how close the trajectory is to the optimal route) decreased with complexity, for chimpanzees and humans alike, as in real-life navigation. Multiple chimpanzees also succeeded with simple open-space mazes. The four chimpanzees completed between 113 and 418 trials in total across some or all of the seven test conditions. Overall, the performance of chimpanzees was often comparable to that of humans. Across environment types, the chimpanzees' travel efficiency resembled that of 3- to 6-year-old children most closely, while the efficiency of older children and human adults was higher. One chimpanzee, Panzee, performed at the level of human adults and even outperformed them in the most complex maze types. The main difference that these virtual studies provided was the capacity for the virtual reality (VR) presentation method to enable dynamic shifts in first-person perspective within the 3D virtual environment such that the viewer's perspective moved with shifts in position. By contrast, most virtual 2D presentations (usually of mazes, viewed from a bird's-eye perspective) were of a fixed environment that did not shift in perspective with a shift in position within the 2D virtual environment, i.e., a static environment (*60*).

The success of some of these maze and joystick studies makes the use of virtual environments one of the most promising avenues for studying primate navigation. To make flexible virtual environments available to a large number of captive primates, be it for scientific or cognitive enrichment purposes (*59*), tasks that are easy to set up, easy to learn, and engaging need to be developed. Computerized testing, in particular with touch screen interfaces, has become widespread in cognitive research with nonhuman primates in captive settings (*61*). In addition, providing naturalistic environments affords the capacity to address a variety of questions that link nonhuman primate behavioral ecology and experimental spatial cognition (*2*, *59*).

As great apes, chimpanzees are a particularly interesting case for studying primate spatial cognition because of the unique foraging challenges that are presumed to have shaped the evolution of their spatial cognition. Chimpanzees have a large body and brain and a relatively costly form of long-distance terrestrial locomotion compared to quadrupedal monkeys (*62*). Chimpanzees cannot consume highly toxic seeds or mature leaves (*63*). To support the metabolic needs of their large brain (in relation to their body size), chimpanzees need to be able to identify and then locate and revisit energy-rich tropical forest foods in varying locations, e.g., large crops of ripe fruit (*29*, *63*). Such food is rare and often widely distributed in space (*63*). In home ranges with seasonal variability, chimpanzees may encounter only one tree with a sufficiently large ripe fruit crop to feed an average-sized chimpanzee group per 10 km of walking (*63*). Such challenges favor individuals who can remember multiple food locations and prioritize their visits to those locations based on food quantity, quality, proximity, and other attributes relevant to foraging efficiency (*64*, *65*). From a welfare perspective, captive chimpanzees may also benefit greatly from the cognitive enrichment that virtual environment games may provide (*66*), given their well-known propensity for creative problem-solving and innovation.

Here, we present the first study of chimpanzees navigating in a rich, virtual open-field environment presented to them to interact with via a touch screen monitor. Within this virtual environment, we created a naturalistic foraging situation in which the chimpanzee learns to navigate toward a distant virtual tree with different types of fruits scattered under its crown. Over a relatively short period of time, we trained six zoo-housed chimpanzees on the basic mechanics for navigating within the game application (app), including the hand-eye coordination for identifying reward items (virtual fruits), changing direction, and orienting to search for new objects. The series of training and testing stages were designed with two overarching aims in mind. Our first aim was to investigate the cognitive processes and behavioral signatures involved in the chimpanzees' navigation through the virtual environment. We focused on two themes that have often been the subject of research on wild primate navigation, namely the use of landmarks for wayfinding and structuring cognitive maps (*7*, *30*), as well as foraging under conditions of environmental variability (*7*, *67*). Specifically, we asked: Would chimpanzees learn to use a virtual "landmark," such as a fruit tree, for orienting? Would they use the same routes repeatedly, and would these become more efficient over time? Would they look for and use a landmark to find familiar locations even when arriving from a different location? Would they reject the landmark

fruit tree as soon as it is clear that it is not bearing fruit, in favor of searching elsewhere, as has been found in wild chimpanzees (*67*)? Our second aim was to relate the chimpanzees' behavioral signatures in the virtual environment to those described in the wild. In particular, we investigated whether navigation trajectories in virtual space could be described using key metrics typically used to describe behavior in natural settings, focusing on path linearity and angular deviation (*23*, *24*, *30*, *68*).

To avoid long training periods, we developed an adaptive training regime in which subjects were always challenged at the level of their current skill, beginning with simple problems. We simulated a foraging situation where the forager discovers a food location, obtains opportunities to revisit and feed at these locations, and, lastly, experiences food depletion and the simultaneous appearance of the same food at novel locations. In this environment, we tested whether chimpanzees would:

1) learn to approach a single visible landmark (a virtual tree) that is in close spatial proximity to virtual food, including when no virtual food is visible;

2) search for and locate this landmark even when it is not visible at the beginning of the trial and when approach requires orienting and/or changing directions;

3) search for and locate this landmark from novel starting locations within the arena;

4) improve goal directedness and path efficiency toward this landmark over time;

5) learn to approach a second, novel goal landmark when the first one is not baited; and

6) learn to avoid the familiar landmark in favor of the new landmark in a strategic manner by aborting a path toward the familiar landmark as soon as it is visible that it is not baited.

MATERIALS AND METHODS

Subjects

Three adult male and three adult female chimpanzees housed at the Wolfgang Köhler Primate Research Center (WKPRC) participated in this study (age M = 28.00, SD = 12.42). All subjects had prior experience with using touch screens, and five of the six subjects had limited experience with 3D video games at the time the study began. All participation was voluntary, and subjects were never deprived of water or food. All research and animal husbandry at WKPRC complies with standards of the European Association of Zoos and Aquaria (EAZA) and the World Association of Zoos and Aquariums (WAZA). For more information, see the Supplementary Materials.

Apparatus

All testing was conducted in the apes' familiar testing areas at WKPRC. The touch screen system is described in detail by Allritz *et al.* (*69*). The virtual reality video game app was run on a Windows PC and was presented to the subject on a Viewsonic monitor [aspect ratio, 5:4; resolution, 1280 × 1024 pixels; frame diagonal, 19 inches (483 mm)] that was mounted outside the testing room at chimpanzee face height (see the Supplementary Materials).

The 3D (virtual reality) video game app ("APExplorer 3D")

The APExplorer 3D app is a virtual reality application that was programmed in C# using the Unity3D game engine. It presents the user with a virtual environment through which an invisible, first-person virtual agent can be steered to explore and interact with objects. All objects in this environment are presented in a 3D cartoon style (Fig. 1). All subjects who participated in this study played in a pure first-person perspective. The invisible agent is guided through the environment by touching any area on the visible screen other than the sky. Upon initiation by touch, the agent starts walking toward the touched location until it has reached that location, until contacting an object with which it can interact, or until a different location is touched, which makes the agent shift direction toward this new location. To allow for a naturalistic navigation experience, regions on the far sides of the touch frame are reserved for instructing the virtual agent to turn on the spot. This means that if the subject makes a touch to these positions on the touch frame, the virtual agent changes orientation, e.g., turns right, without walking at the same time (see the Supplementary Materials). As the subject moves the agent through the virtual environment, the visual perspective shifts accordingly, creating a realistic movement of perspective as in the real world. The subject is in control of where to go and where to look. Objects look closer as they are approached, and solid objects (e.g., trees or rocks) must be circumvented to get to the other side. All walking was accompanied by the sound of footsteps to provide an additional layer of interactive feedback. The sound of footsteps signals that the agent is still moving in response to the user's input;

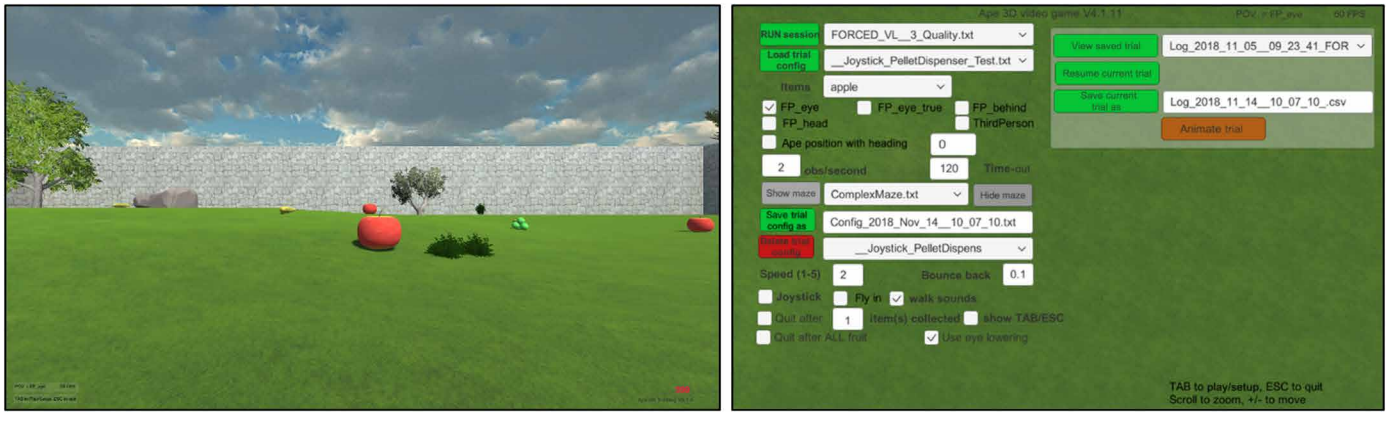

Fig. 1. The APExplorer 3D app. (**Left**) Example of an exploration trial. (**Right**) Setup mode that allows the researcher to control different parameters, such as walking speed, perspective, head orientation, and others.

when the sound of footsteps stops, this signals that the agent is waiting for input. This feedback can be registered by the user even when they are momentarily not looking at the screen.

All training and testing trials were conducted in a square, park-like arena surrounded by walls. This arena presented subjects with multiple obstacles, such as rocks, trees, fences, and a big lake in the east (see fig. S1). Upon walking into the walls or any of the obstacles (including the lake), the virtual agent is bounced back slightly (by 0.5 m in the game). In addition to obstacles that serve as physical barriers, the arena also contains some objects ("bushes") that can occlude other objects and locations but which the agent can walk through. Last, the arena also contains two shallow hills, one in the central north of the arena and one in the far northeast.

In setup mode, the researcher may scatter any of six available types of food (mostly fruits, like apple, banana, grapes, and mango, as well as peanut and honeycomb; see Fig. 1) within the arena. When playing the game, the chimpanzee can collect these foods: Upon walking close enough to a virtual food item, a sound signals success ("tadaa"), and the virtual food is briefly lifted into the air, shakes, and then disappears. The experimenter can choose the time the user is allowed to explore and forage within the environment until the trial times out, and the experimenter may select different walking speeds. The arena covers a virtual area of 100 m by 100 m, and the virtual agent's speed was set to 2.5 m/s for this study.

The data collected with APExplorer 3D include 3D coordinates of the virtual agent's position that can be sampled at different rates (in this study, one update of the agent's location approximately every 500 ms). In addition, the software records when and in which location a fruit item was collected and at what point in time which part of the arena was touched by the chimpanzee.

Trial procedure

The chimpanzees' task on all trials was to find and collect multiple pieces of food within the allotted amount of time (always 150 s). Each trial contained four or five pieces of food positioned in close proximity in a specific location within the arena. Arriving at this location was thus typically rewarded with multiple pieces of food that could be collected one at a time. Each trial began with an initiation screen. When the chimpanzee touched a start icon on the screen, a trial began. The program switched to game mode, presenting the arena from the virtual agent's perspective, beginning in the starting location preset for this trial (x, y, and z coordinates) with a preset head orientation (between 0° and 360°, with 0° for an agent that faces north). Each trial presents multiple food icons, including bananas, apples, and grapes. Whenever the subject collected a piece of food within the game, the reward routine played (see above). The experimenter provided a real piece of the corresponding fruit (one grape, piece of apple, or slice of banana). If all pieces of food were collected before 150 s had passed, the trial ended, and the chimpanzee was free to initiate the next trial. If the chimpanzee did not collect all pieces of food, the trial timed out, and they could initiate the next trial. Figure S1 presents an example trial from the setup perspective and from the virtual agent's perspective once the subject initiated the trial. Movies S1 to S4 present multiple example trials from different stages.

Session procedure

Each chimpanzee participated on multiple testing days. On each testing day, a subject completed up to three "sessions," where each session consisted of three or four trials that presented a similar challenge. For example, one such challenge may be to find food that is located in a constant location, with the virtual agent starting from a familiar position at the beginning of each trial, while only the head orientation of the agent varied across trials. Each individual completed up to nine trials per day.

Experimental design

All subjects completed an "exploration" period before the study, in which they learned to control the app (see the Supplementary Materials). This ensured that each ape could discriminate targets on the screen and could rotate the invisible agent left and right and bring it into contact with a nearby visible target. The study that followed consisted of four phases. The first three phases, jointly referred to as "location learning," presented an adaptive training procedure. Subjects progressed through three phases of increasing difficulty to navigate toward a fixed goal location. This location was associated with a fixed landmark, namely a "treasure tree," which had fruit items (which the chimpanzees already had become familiar with) scattered under its crown (in the fruit fall area). The fourth, final phase, referred to as the "new location test," was a fixed progression of 12 identical sessions that consisted of baseline, training, and probe trials to monitor how quickly subjects would learn to approach a novel goal location with hidden food.

Location learning

The goal of this adaptive training procedure was for subjects to learn to navigate toward a fixed goal location. Location learning consisted of three training phases, in which the chimpanzees learned to approach the initial location from varying (i) distances, (ii) orientations, and (iii) starting locations (see Table 1).

Each of these three phases was further subdivided into stages. For example, phase 1 ("distance") was subdivided into multiple stages (1A, 1B, and 1C) that differed with regard to the distance between starting location and goal. When a subject entered a new stage, they were presented with at least one session of this stage. A session refers to a block of three trials for all stages of location learning. For example, a session of stage 2A (the first stage of phase 2, "orientation") consisted of one trial in which the subject faced the goal location tree at trial start, followed by a trial in which the subject faced 90° to the left, followed by a trial in which the subject faced 90° to the right (see Fig. 2). Subjects had to successfully complete at least two of the three trials in a given session to be promoted to the next stage. A full list of maps for all phases, their stages, and trials can be found in the "Trial configurations overview" section in the Supplementary Materials.

On each training day, a subject received a maximum of three sessions. On each trial, subjects could collect up to five pieces of food within the time limit. A session was counted as successful if at least one piece of food was collected in at least two trials of that session.

The general progression through the different stages was as follows: 1A ➔ (1A+) ➔ 1B ➔ (1B+ ➔ 1B++) ➔ 1C ➔ 2A ➔ 2B ➔ 3A ➔ 3B ➔ 3C. Parentheses indicate stages that were interjected only if a subject failed on their first attempt at the stage that would follow it. On the first training day, subjects started with a session of stage 1A. On any day that followed, the subject started with a session of the last successful stage from the previous day. In stages of phase 1 (1A, 1A+, 1B, 1B+, 1B++, and 1C), the agent always faced the goal location tree on each trial; stages differed only with regard to how

Table 1. Learning phases in location learning period.

Phase	Challenge	Description	Stages
Phase 1	Distance	Subjects learn to walk directly to a goal location (a cluster of fruit) that was close to a fixed landmark ("fruit tree") in the north of the arena.	Stages: 1A, 1A+, 1B, 1B+, 1B++, and 1C. Each stage consists of three identical trials. Subject begins every trial directly facing the "fruit tree" landmark, but the distance between starting location and goal location landmark increases across stages. In early stages (1A, 1A+, and 1B), landmark *and food* are visible at the beginning of each trial; in later stages (1B+, 1B++, and 1C; see main text), only the landmark (top of the tree) is visible at the beginning of each trial. Stages with a "+" in their name were only interspersed when necessary (see description below). Walking distances from start to goal area differed between all six stages and ranged between about 25 and 70 virtual meters across stages, with earlier stages putting the agent closer to the goal. This means that minimum walking durations from start to collecting the first piece of fruit ranged between about 10 and 30 s.
Phase 2	Orientation	Subjects need to rotate or turn in some trials to locate the same landmark as before.	Stages: 2A and 2B. Trials in each stage always begin in the same starting location as trials in stage 1C (no food visible), allowing the subject to follow their learned trajectory, but trials differ with regard to the viewing direction of the virtual agent at the beginning. The agent faces the tree directly in some trials but is facing 90° left, right, or the opposite direction in other trials. Walking distance is identical to the final stage of phase 1, requiring at least about 30 s of walking to collect fruit.
Phase 3	Starting location	Subjects need to rotate or turn in some trials to locate the same landmark as before and approach it from different starting positions than in phase 2.	Stages: 3A, 3B, and 3C. Each of three trials within each stage places the virtual agent in one of three possible starting locations: Trial 1 places the agent in the east, trial 2 in the west, and trial 3 in the south of the map at trial start. Starting orientations in each of these trials vary across the different stages. Required walking distance ranged between about 50 and 100 virtual meters, requiring walking durations of between about 20 and 40 s.

distant the starting location was from the goal location (1A, 15.8 m; 1A+, 27.6 m; 1B, 36.5 m; 1B+, 41.4 m; 1B++, 45.7 m; 1C, 61.5 m). As a consequence, in stages 1A, 1A+, and 1B, both the tree and the fruit underneath its crown were visible from the moment a trial was initiated, whereas in stages 1B+, 1B++, and 1C, only the top of the tree was visible when the trial began. In stages of phase 2 (stages 2A and 2B), the starting location was always identical to the starting location farthest away from the goal in phase 1 (that is, stage 1C, or 61.5 m), but now, the agent's head faced different directions across trials, requiring the subject to locate the goal tree first before approaching it (see the "Trial configurations overview" section in the Supplementary Materials). Last, across stages of phase 3, the agent was placed in different starting locations across trials (see the "Trial configurations overview" section in the Supplementary Materials).

Which two sessions followed the first one on a given training day was determined by a set of promotion and demotion rules designed to keep the task challenging but manageable for subjects (Supplementary Materials). There was no break between testing sessions beyond the time it took to determine which session the chimpanzee would receive next, based on their performance. Each testing day stopped after three sessions had been run or if a subject lost interest in participating. As soon as a subject had passed stage 3C, no further sessions were run on the same day, and the subject began with the new location test (phase 4) on the next testing day.

New location test

The goal of this fixed progression of identical test sessions was to rigorously assess how quickly subjects would learn to navigate to a novel goal location. A second goal was to assess how flexibly

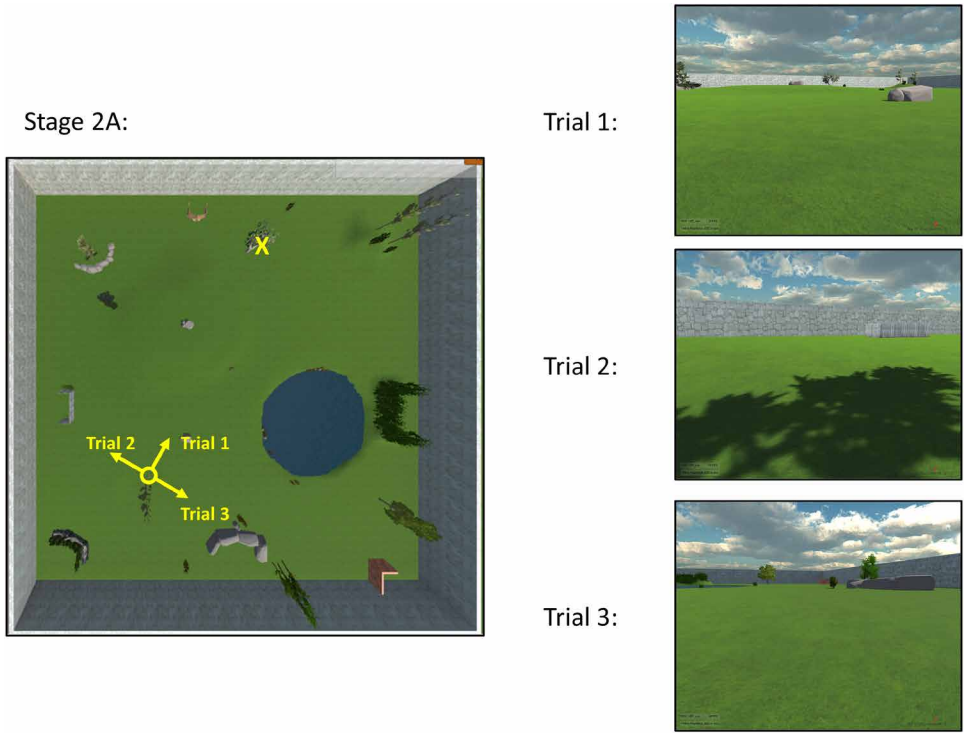

Fig. 2. The three trials of a session of stage 2A, which was the first stage in phase 2 (orientation). (**Left**) Bird's-eye view of starting orientations and starting location for all trials. (**Right**) Virtual agent perspectives at the beginning of each trial.

the chimpanzees would respond to the visible absence of food at the original location, that is, whether they would still travel until they had arrived at the—now visibly empty—original goal location, or whether they would abandon this plan in favor of the alternative location as soon as it could be seen that the original location was not baited. Unlike previous phases, phase 4 was not subdivided into different stages. Furthermore, unlike in all previous stages (stages 1A to 3C), each session of phase 4 consisted of four rather than three trials. Each subject was presented with the same session, that is, a block of four trials, 12 times (Fig. 3). Each subject completed up to two of these sessions per day. Trial 1 of each session was a baseline trial, that is, a trial with the familiar goal location and the final starting location and head orientation from phase 1 (that is, identical to a trial from stage 1C). This baseline trial was followed by three trials with a new, hidden goal location. In these trials, a cluster of four pieces of food was hidden behind the small hill in the northeast of the arena (see Fig. 3 and the "Trial configurations overview" section in the Supplementary Materials). Thus, each of these trials (trials 2 to 4 of each session) used the same new goal location. In addition to the food in this new location, the first two of the new-location trials (trials 2 and 3 of each session) presented subjects with an additional food item that was visible just before arriving at the familiar but now empty goal location. This additional food item was meant to serve as a hint to guide subjects toward the novel hiding location (training trials). In the final of the three new location trials (trial 4 of each session), no such hint was provided. These trials (trial 4 of each session) will be referred to as probe trials.

Analyses

Location learning

The analyses addressed three main questions. First, we addressed the question whether each ape solved the basic task posed in phases 1 to 3, as evidenced by meeting the criterion in all three phases. To answer this question, we assessed how quickly subjects adapted to find the same location in trials of different phases (distance, orientation, and starting location), quantified as the number of trials it took to complete the different phases.

Second, we analyzed how walking trajectories developed over time. For trials of phase 1, for which we collected a larger number of data for most individuals, we analyzed movement and orientation data in the same way as has been done in natural settings (*23*, *24*). We monitored how "walking" efficiency developed across trials, using two well-established indices: path linearity and angular deviation at the beginning of travel. Path linearity describes the ratio of "the length of the optimal route from a starting point to a goal location" and "the actual route traveled toward that goal location." Thus, linearity is only defined for successful trials and is bound to be larger than zero and smaller or equal to one. "Success" in these analyses refers to subjects reaching the "fruit fall area," defined here as the region that contains the tree and the five pieces of fruit, encompassing an area of about 28 m^2. Angular deviation is the difference in bearing between a straight line that represents the beginning of the optimal route toward a goal and a straight line that approximates the beginning of the actual route. We calculated these angles in such a way that clockwise deviations ranged from 0 to 180, and counterclockwise deviations ranged from 0 to −180. For a

Fig. 3. The three types of trials that comprised each session in phase 4.

detailed description of our calculations of path linearity and angular deviation in all conditions, see the Supplementary Materials.

We predicted more efficient navigation (increasing path linearity values and decreasing angular deviations across trials) for later trials of phase 1, considering separately those trials in which subjects saw the fruit at trial start (stages 1A, 1A+, and 1B) and those in which they did not (stages 1B+, 1B++, and 1C). To analyze whether path linearity increased across those trials of phase 1 in which subjects did not see the fruit at trial start, we fitted a generalized linear mixed model (GLMM) with beta error structure and logit link function (using the R package glmmTMB). To analyze the relationship between trial number and angular deviation, an analogous model was fitted that predicted relative deviation, ranging between zero and one, and disregarding whether the deviation was to the left or to the right of the optimal path to the goal; see (*23*). For details of all models, see the Supplementary Materials.

Recall that subjects were promoted from a specific stage to the next one as soon as they had become sufficiently successful, which gave them little opportunity for improving path efficiency within a given stage. To examine changes in linearity and angularity across a larger number of identical trials, we also analyzed, in a separate step, a larger set of trials of type 1C. This included the initial administration of stage 1C that was part of location learning (between 3 and 27 available trials per subject, of which between 3 and 10 were successful) but did not include any other trials from phase 1 (that is, it did not include trials of types 1A through 1B++). The analysis also included the identical baseline trials (type 1C) that subjects completed as the first trial of each session of phase 4 (12 available trials per subject, of which between 10 and 12 trials were successful). We fitted a group-level model analogous to those described above. In addition, we also fitted individual-level models that predicted linearity as a function of trial to assess whether the walking efficiency of individual subjects improved over time. Rather than hypothesis testing, this analysis was exploratory as no clear prediction could be made for the baseline trials that subjects encounter in phase 4. One prediction might be that further repetition results in further improvement. Alternatively, each baseline trial in phase 4 is followed by three others in which the old goal location is empty, making it ultimately more difficult to predict whether following the usual path will pay off.

In a third set of analyses of the location learning phase, we report success rates in trials of phase 2 (orientation) and phase 3 ("starting location"). Because subjects passed through these stages very quickly and thus the number of data points for each unique trial was very small, we only report descriptive statistics for these phases.

New location test

Foragers often encounter situations in which familiar food locations are depleted, and they have to use visual cues and/or spatial memory to take advantage of additional resources. To simulate this kind of situation, we included the new location test. We addressed two main questions about subject performance in probe trials of this test. First, we tested whether subjects became more successful across trials. We fitted a GLMM with binomial error structure and logit link function (R package glmmTMB, function glmmTMB) that predicted success as a function of trial (for details, see the Supplementary Materials).

Second, we tested path efficiency similarly to phase 1. At the beginning of any given trial in phase 4, a subject, unless they are counting trials, cannot know whether they are facing a trial in which food can be found in the old versus the new hiding location until they have seen at least one of the two locations. This needs to be disambiguated. In probe trials, a less efficient method would thus include walking all the way to the empty old location and from there toward the new location. A more efficient method would be changing course as soon as it becomes clear that the old location is empty.

We thus predicted that increasing path efficiency may not be expressed in improving path linearity as considered from the actual starting location but only when considering paths starting from the first position along the total trajectory from which it can be determined that no food is hidden in the old goal location. Points of this type form a line across the arena, which is depicted in Fig. 4, and which will be referred to as the disambiguation line. Its shape and location result from the idiosyncratic combination of elevation levels and obstacles in the testing arena, simulating a natural foraging situation. From the disambiguation line, the ape could not see the hint food (if any) or the food (if any) at the new location. In line with

the hypothesis that the chimpanzees would decide earlier—across trials—when to abandon a route toward the original goal location, we thus predicted linearity from the disambiguation line toward the second goal (Fig. 4, vector B) to increase across successful trials and fitted a GLMM analogous to the ones fitted for phase 1 (Supplementary Materials). This second goal was defined as the region that contains the hill with the two trees and the four pieces of fruit, encompassing an area of about 31 m^2. We also analyzed angular deviation to test whether travel decisions changed over time. For each trial, we estimated the optimal path from the subject's intersection with the disambiguation line toward the new goal location and calculated the angular deviation from this path as before. Only for this analysis of phase 4 did we also include the baseline trials. To test the hypothesis that subjects would become more efficient over time, we fitted a GLMM that predicted relative angular deviation as a function of trial, trial type (goal in location 1 versus location 2), and their interaction as fixed effects. If the chimpanzees learned over time to settle—as soon as they see that location 1 is not baited—on a straight path to location 2, we would expect an interaction effect. Angular deviation from the optimal path to the new goal should become smaller in probe trials but should become larger or remain the same in baseline trials (for more details, see the Supplementary Materials).

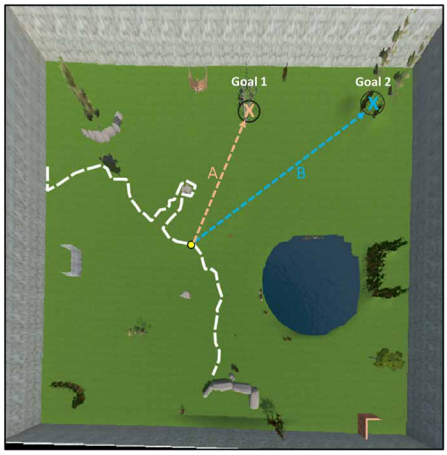

Fig. 4. Disambiguation line in trials of phase 4. The disambiguation line (dashed, white line) separates those areas in the arena from which the virtual agent can see whether food is present in the original goal location (north, goal 1) from those areas from which this cannot be determined. Yellow dot represents a hypothetical point at which a subject's path may intersect with this line. Vectors A and B represent approximate optimal routes toward each of the two goals if starting from this intersection point.

RESULTS

Phases 1 to 3: Location learning

Progression through stages

All six chimpanzees were able to solve the basic tasks in phases 1 to 3. By the end of phase 3, each chimpanzee was able to use the touch screen to bring the invisible agent into contact with a virtual food icon. Furthermore, each ape could do so in conditions in which the food was not directly visible from the starting position, when the agent had to be navigated for more than just a few seconds, and when the goal distance, head orientation, and starting location varied across trials.

Table 2 depicts the number of sessions that each subject completed in each of the 12 stages (from 1A to 4). On average, subjects completed ca. 15 sessions of phase 1 (M = 14.83, SD = 8.08), ca. 4 sessions of phase 2 (M = 4.17, SD = 0.98), and ca. 5 sessions of phase 3 (M = 5.33, SD = 1.37). Numerically, subjects required more time mastering those stages of phase 1 in which they could not see the food but only the fruit tree at trial start (because the view was covered by a hill between the virtual agent and the food; sessions completed: M = 4.67, SD = 2.66 for stages in which food could be seen at trial start and M = 10.17, SD = 6.79 for stages in which food could not be seen at first; see also Fig. 5), and the increased difficulty of finding the food once it was not visible anymore at the beginning of each trial also resulted in larger variation in linearity and

Table 2. Number of sessions of each stage completed by each subject. m, male; f, female.

Stage	Alex (m)	Dorien (f)	Fraukje (f)	Frederike (f)	Lobo (m)	Lome (m)
1A	1	4	1	1	1	1
[1A+]	0	2	0	0	0	0
1B	2	4	3	3	3	2
[1B+]	1	6	4	2	5	0
[1B++]	2	4	4	1	6	0
1C	3	3	6	4	9	1
2A	2	3	2	1	1	3
2B	2	2	3	2	2	2
3A	1	1	3	2	1	3
3B	2	3	1	3	2	1
3C	1	1	1	3	2	1
4	12	14*	14*	12	12	14*

*Note that for three subjects, two sessions were repeated because data for at least one trial were lost because of a program error. For more details, see the Supplementary Materials.

angular deviation (see below). For video examples of trials from all three phases, see movies S1 to S3. Figure S3 presents example trajectories from all three phases for one subject.

Efficiency of walking trajectory to reach fruit fall area in phase 1 (distances)

Linearity. Figure 6 depicts path linearity across stages and trials for each subject for successful trials, that is, those in which subjects reached the fruit fall area eventually. In conditions in which subjects could see the fruit at the beginning of the trial (top row of Fig. 6), the median linearity score ranged between 0.99 and 1 across the six subjects, that is, the subjects took a direct route in most cases. In conditions in which subjects could not see the fruit at the beginning of the trial (bottom row of Fig. 6), the median linearity score ranged between 0.58 and 0.88 across the six subjects. For details, see the Supplementary Materials.

Angular deviation. Patterns of angular deviation mirrored the linearity patterns (fig. S7). In trials in which food was visible from the beginning (stages 1A to 1B), the median absolute angular deviation from the optimal path was 14.67°; subjects took a direct route toward the visible food in most cases. In conditions in which subjects could not see the fruit at the beginning of the trial (bottom row of fig. S7), angular deviation fluctuated substantially between and within subjects (see fig. S7). For details, see the Supplementary Materials.

Efficiency of walking trajectory to reach fruit fall area across all trials of type 1C

Linearity. We explored whether path linearity improved further over time by analyzing the full set of available trials of type 1C, in which subjects saw the distant landmark but not the food at the beginning of the trial. We analyzed only those trials in which subjects reached the fruit fall area, this time including both the initial administration of stage 1C that was part of location learning and the identical baseline trials that subjects completed at the beginning of each session of phase 4. The results of this analysis are depicted in Fig. 7. Individual median linearity scores ranged between 0.57 and 0.89 in the initial phase of the experiment (stage 1C) and between 0.62 and 0.99 in identical trials that were presented in the last stage (phase 4). Individual analyses revealed a significant positive increase in path linearity for three subjects (all $P \leq 0.016$), nonsignificant linearity increases in two subjects ($P = 0.052$ for male Lobo and $P = 0.446$ for female Frederike, respectively), and a significant decrease in linearity only for female Dorien ($P = 0.036$). For our sample of six chimpanzees, considered as a group, there was a tendency for paths toward the goal to become more linear across successful type 1C trials, although this did not reach conventional levels of statistical significance [$N = 6$, $\beta = 1.51$, $\chi^2(1) = 3.28$, $P = 0.070$].

Angular deviation. Relative angular deviation from the optimal path to the goal was marked by substantial variation across trials for all but one subject in phase 1 (circles in fig. S8). There was also substantial variation in angular deviation across phase 4 baseline trials (triangles in fig. S8). Individual Pearson correlations between trial and deviation were negative and ranged between −0.07 and −0.71 for all but one subject (female Frederike, $r = 0.31$). On the individual level, GLMs revealed a significant negative effect (such that later

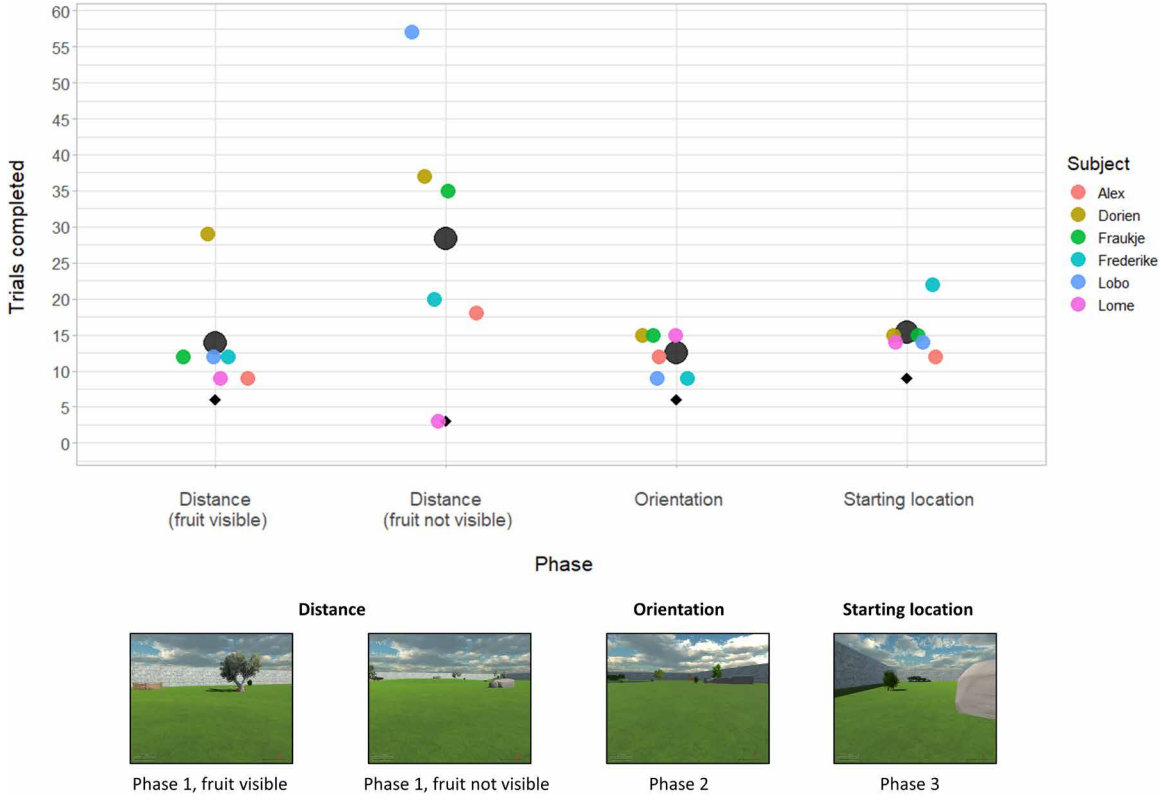

Fig. 5. Trials of different phases completed by each subject. Each phase name refers to a specific challenge: varying distances, varying starting orientations, or varying starting locations across trials of the phase. (**Top**) Individual and group data. Black bubbles represent group mean. Diamonds represent the minimum number of trials required to complete each phase without any repetitions or demotions. (**Bottom**) Starting views of virtual agent in example trials of each condition.

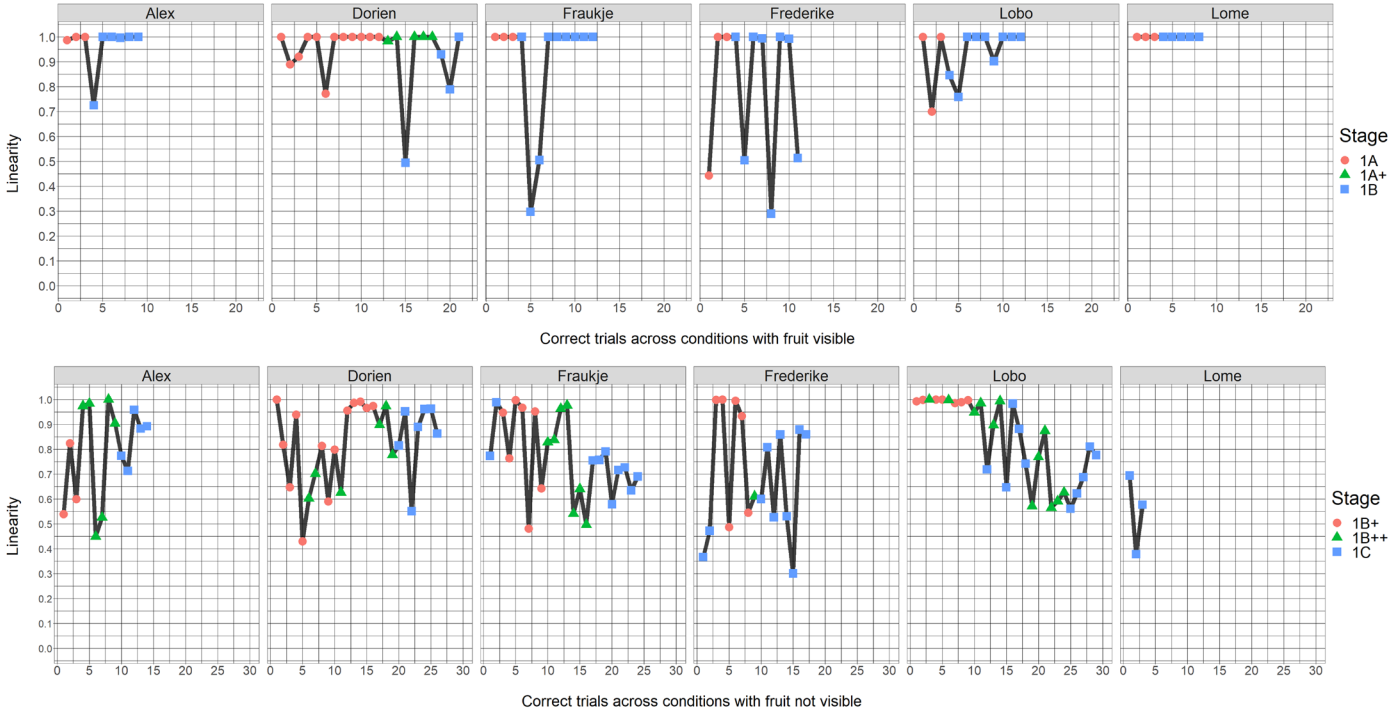

Fig. 6. Path linearity across trials of phase 1 (distance). (**Top**) Stages 1A, 1A+, and 1B. Food was visible from the virtual agent's starting point in all trials. (**Bottom**) Stages 1B+, 1B++, and 1C. Food was not visible from the agent's starting point in any trial. Figure includes only successful trials.

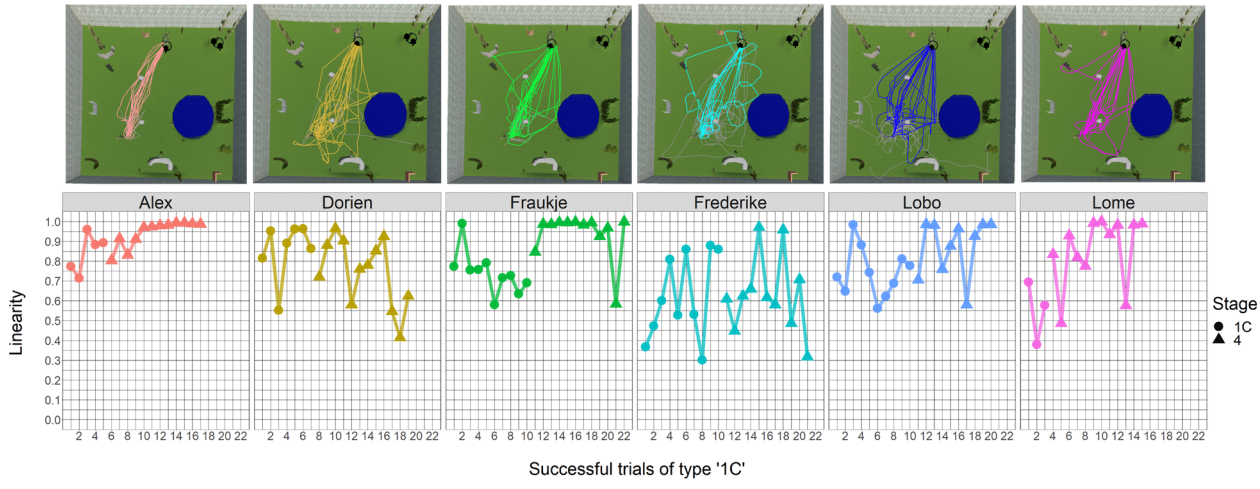

Fig. 7. Path linearity across all successful trials of type 1C. Trials are from stage 1C (circles) and from stage 4 (triangles).

trials showed smaller deviation from the optimal path) for two subjects, male Alex [Pearson correlation $r = -0.71$, GLM: $\beta = -0.53$, $\chi^2(1) = 14.55$, $P < 0.001$] and female Fraukje [Pearson correlation $r = -0.31$, GLM: $\beta = -0.43$, $\chi^2(1) = 5.63$, $P = 0.018$]. For the sample of six chimpanzees, considered as a group, the effect of trial on angular deviation was in the expected direction but not significant [$N = 6$, $\beta = -0.15$, $\chi^2(1) = 2.57$, $P = 0.109$].

Success in phases 2 and 3

Phases 2 and 3 presented the chimpanzees with two new challenges, changes in the agent's initial orientation and in its initial location. A full breakdown of starting locations and orientations can be found in table S5 and in the "Trial configurations overview" section in the Supplementary Materials.

In each trial of phase 2, the agent started in the same location as it did in the final trials of phase 1; however, trials differed with regard to the agent's initial orientation, which was either set to default (facing the tree) or shifted 90°, 180°, or 270°, requiring the chimpanzee to turn the agent before approaching the goal. All subjects passed through the two stages of phase 2 within 9 to 15 trials. Chimpanzees did not do equally well on all trials, however: In trials in which the agent's initial orientation was shifted 90° to the right with respect to the default orientation, the mean success rate (collecting at least one

piece of fruit) across subjects was 52.5%, whereas on the three other types of trials, success ranged between 83.33 and 89.17%.

In each trial of phase 3, the agent started in one of three novel starting locations (east, west, and south). Across stages, trials additionally differed with regard to which direction the agent faced initially, such that, e.g., stage 3A included a trial in which the agent started in the east location facing west; stage 3B included a trial in which the agent also started in the east location but facing east and so forth (see table S5). Subjects passed through the three stages of phase 3 within 12 to 22 trials. Trials in which subjects started in the south location, surrounded by a rock formation that they needed to circumvent to get on a path toward the goal tree, proved particularly difficult; mean success rates for these trials ranged between 27.78 and 33.33%, whereas success rates in all other trials ranged between 77.78 and 100%. For a full breakdown of individual success rates in trials of phases 2 and 3, see table S6. Because of the quick pace with which all subjects succeeded in phases 2 and 3 and, as a result, the small number of data points for each unique trial, no analyses were conducted of how path efficiency developed over time.

Phase 4: New location test

Success across no-hint probe trials

Figure 8A depicts success (collecting at least one piece of fruit) in no-hint probe trials over time. For chimpanzees as a group, there was a positive effect of trial [$N = 6$, $\beta = 1.25$, $\chi^2(1) = 9.33$, $P = 0.002$]; subjects became more successful over time. For a video example of a phase 4 trial, see movie S4.

Efficiency of walking trajectory to reach fruit fall area across no-hint probe trials

Linearity. Across subjects, there were 33 successful no-hint probe trials in total. With regard to path linearity within the section of the trajectory that lay beyond the disambiguation line, there was no effect of trial [$N = 6$, $\beta = 0.24$, $\chi^2(1) = 1.56$, $P = 0.212$]. That is, across the relatively small number of successful trials in this dataset, subjects' path linearity toward the novel goal location did not significantly improve. Maximum linearity and variability of linearity differed substantially between subjects. Four subjects succeeded on 6 or 7 of the 12 trials. Of these, one subject exhibited high linearity from the first successful trial on (male Alex, median linearity = 0.94), while another gradually improved across successful trials [male Lobo, individual effect of trial: Pearson $r = 0.84$, GLM: $\beta = 0.88$, $\chi^2(1) = 7.87$, $P = 0.005$]. The two remaining subjects (female Dorien and male Lome) exhibited medium linearity across the trials (0.54 and 0.71, respectively). As can be seen in the top row of Fig. 8B, these two subjects used an indirect but fairly consistent route on multiple occasions: They traveled all the way to the old but empty goal location and further northeast toward the wall of the arena. From there, they reoriented and walked southeast toward the

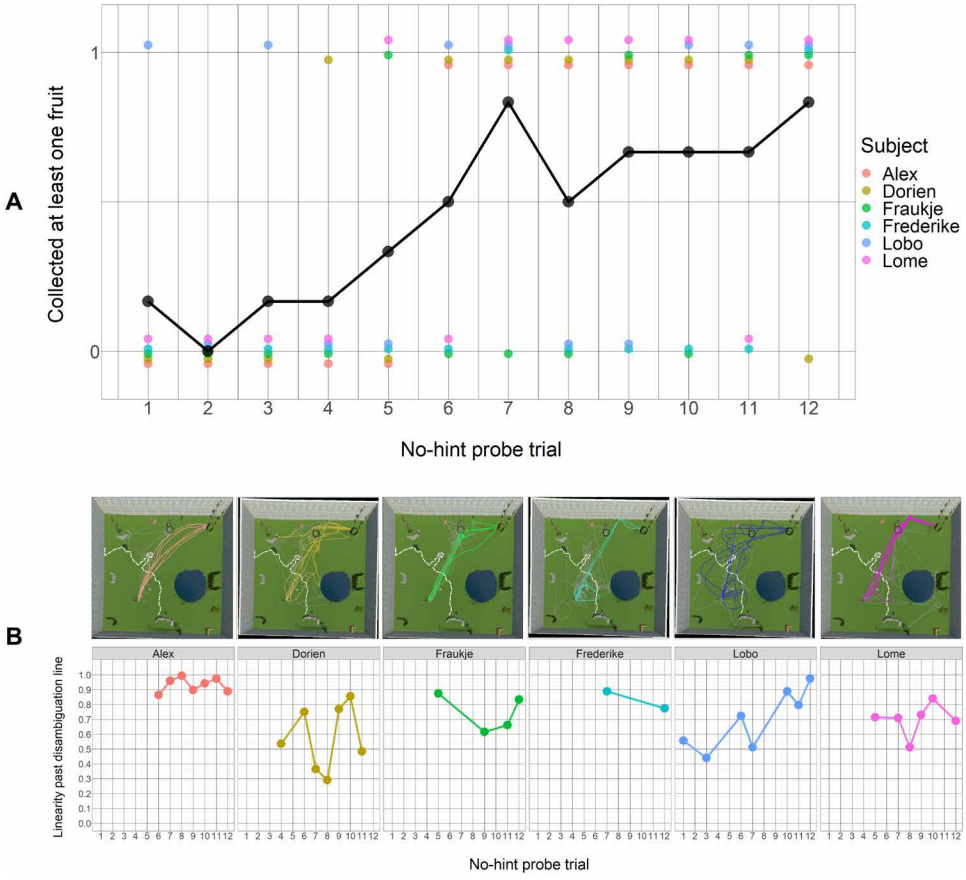

Fig. 8. Performance across no-hint probe trials of phase 4. (**A**) Mean and individual success in collecting fruit across trials. Individual results are depicted in color; mean accuracy is depicted in black. Individual values are slightly shifted away from zero and one to increase readability. (**B**) Linearity beyond disambiguation line in successful trials. Top: Paths in trials that were eventually successful (bright colors) and in trials that timed out (gray). Dashed white line represents the disambiguation line. Bottom: Linearity across successful trials.

novel goal location, as the fruit in this location was visible from there. All but one of the other subjects also used a variation of this route in at least one trial.

Angular deviation. We compared how angular deviation toward the new goal, as seen from where the subject intersected the disambiguation line, developed across trials, contrasting baseline and probe trials. There was no interaction effect between trial type and trial [$N = 6$, $\beta = -0.16$, $\chi^2(1) = 1.08$, $P = 0.299$]: Angular deviation toward the new goal did not decrease more strongly across trials in which the old goal was not baited. An exploratory reduced model that excluded the interaction effect did not reveal sizable main effects for trial type [$\beta = 0.04$, $\chi^2(1) = 0.05$, $P = 0.828$] or trial [$\beta = -0.09$, $\chi^2(1) = 1.23$, $P = 0.267$]. We did not find significant interaction effects for individual subjects. In summary, while several subjects became more successful over time in finding the new goal location eventually, as a group, they did not gradually begin to approach the new goal more directly across the 12 trials that we administered, a finding that is consistent with the variability in linearity and the taking of alternative paths described in the previous section (see fig. S9).

DISCUSSION

In this study, we presented captive chimpanzees with a virtual environment foraging task that simulated foraging challenges encountered by conspecifics in their natural habitat. Our primary aim was to investigate the cognitive processes and behavioral signatures involved in the chimpanzees' navigation through the virtual environment. The chimpanzees learned how to play the game with a touch screen over the course of a few weeks. They then progressed quickly through different stages. Relating the results to our research questions, we found the following:

1) All six tested chimpanzees learned to approach a single visible landmark (a virtual tree) that was in close spatial proximity to virtual food (stages 1A to 1C). They also succeeded when no virtual food was visible (stages 1B+, 1B++, and 1C: distances), but most subjects needed more time to succeed on this latter challenge.

2) All six chimpanzees searched for and located this landmark even when it was not visible at the beginning of the trial and when approach required orienting and/or changing directions, as evidenced by their high success rates in phase 2.

3) All six chimpanzees searched for and located this landmark from novel starting locations within the arena, as evidenced by their high success rates in phase 3.

4) Three chimpanzees improved goal directedness and path efficiency toward this landmark over time, as evidenced by an increase in path linearity across trials of type 1C, whereas two individuals showed nonsignificant results, and one individual showed an opposite result, with her paths becoming less linear, when trials were intermixed with trials in which the new landmark was baited.

5) Considered as a group, the chimpanzees learned to approach a second, novel goal landmark when the first one was not baited, as evidenced by an increase in success across no-hint probe trials of phase 4; however, there were clear individual differences with regard to the number of successful trials and with regard to improvements in path linearity.

6) Only one chimpanzee learned to avoid the familiar landmark in favor of the new landmark in a strategic manner by aborting a path toward the familiar landmark as soon as it was visible that it was not baited on multiple trials (male Alex). For one individual, linearity gradually improved across successful trials (male Lobo), while several others repeatedly showed an alternative strategy of using the original landmark as a beacon from which they reoriented to find the new landmark.

These results will be further discussed below. In addition to the finding that most chimpanzees solved most of the navigation challenges that we gave them, it stands out that they did so rather quickly when compared with the extensive training times associated with some types of touch screen tasks that use static stimuli, which may require months of training with thousands of trials for nonhuman primates, e.g., color discrimination (*69*), transitive inference (*70*), and relational matching (*71*). The current finding of rapid adjustment to a navigation problem is consistent with results from other computer-presented spatial tasks (*46*, *48*). These results, considered together, suggest that more ecologically enhanced open-field virtual environments that are navigated via touch screen provide great potential for studying cognition, in particular, navigation in primates and other taxa.

Whether wild chimpanzees use distinct landmarks to locate familiar food sources has been the subject of multiple field studies. In the wild, chimpanzees show goal-directed travel toward food trees with remarkably high measures of linearity to feed on and monitor food sources (*7*, *30*). For example, Janmaat *et al.* (*7*) found that wild chimpanzees were more likely to perform goal-directed travel to large landmarks, such as large feeding trees.

Similarly, the chimpanzees in the current study were able to learn, across the later stages of phase 1 (distance learning), to identify a specific virtual landmark as an indicator of where food was hidden (result 1). The chimpanzees did not simply succeed by habitually doing what they had done before. When they could not see the virtual food anymore in phase 1, but only the landmark, most of them required more trials before they succeeded, and their initial trajectories, even on successful trials, showed less linearity and stronger deviation from optimal paths than in earlier trials in which food was visible from the beginning. This mirrors a common assumption in primate movement ecology, namely that direct visual or olfactory access to cues or goals, e.g., smelling fruit or seeing a familiar tree, will result in more linear paths and faster travel (*10*, *25*, *72*, *73*). Viewing our results through this lens, the virtual fruit icons that were visible in early stages of phase 1 (apples, banana, and grapes) were already quite familiar to all subjects from their exploration training sessions (see the Supplementary Materials) and could therefore serve as a beacon from the very first trial. The tree under which the fruit was located, on the other hand, gradually acquired its affordance, that is, to serve as a beacon, over the course of the study. Once the chimpanzees appeared to have learned that this tree could serve as a landmark that signaled the presence of food, however, the transfer to succeeding from new starting locations and orientations was almost instantaneous, and subjects often passed through multiple consecutive stages without repetitions (results 2 and 3). This further indicates that it was the specific landmark, rather than, e.g., tapping the touch screen in a specific location, that subjects learned to associate with locating food. This is consistent with the use of positive and negative landmarks by apes navigating virtual 3D mazes in previous studies (*49*, *59*).

Using landmarks as beacons to find familiar locations coming from different directions has also been reported for wild primates. For example, wild capuchins (*Cebus capucinus*) use landmarks to locate food in small-scale space (*74*). Regarding large scales, one study of bearded capuchins (*Sapajus libidinosus*) found that route

nodes, locations at which individuals make directional changes, are associated with locations where they have increased visibility over the landscape (*28*). Furthermore, wild chacma baboons (*Papio ursinus*) make large detours to surpass neighboring groups, but only when prominent landmarks are visible, when they are traveling on a hill. Smaller detours were detected when baboons were traveling on the plain where they could not see these landmarks (*10*). Similarly, the chimpanzees in our study used the (northern) fruit tree as a landmark to make sense of their environment. Phase 2 required the chimpanzees to turn the agent on the spot or walk in circles before they could even see the tree, a requirement that all subjects met on most trials (result 2). Last, in phase 3, the chimpanzees were able to use the tree to find the food even when coming from locations in the arena that they had rarely or never been in before (result 3).

In the new location test, the chimpanzees were challenged with a certain degree of unpredictability, as often occurs in the wild. The chimpanzees adapted quickly: As a group, they became more proficient in finding the fruit in each probe trial in which no food was in the original location (result 5). However, individuals used different strategies to succeed. One subject (male Alex) learned quickly to use the hill and tree in the northeast of the arena as an additional landmark that could guide him directly to the food that was hidden there in probe trials. Other subjects used a less direct strategy in which they used the original goal location as a beacon, even when it was visibly empty, from which they then reoriented to discover the food behind the hill in the northeast. Although this behavior was somewhat unexpected by the experimenters, this route consistently led these chimpanzees to success (result 6).

Consequently, we did not find conclusive evidence regarding our final hypothesis that the chimpanzees would learn—across trials—to avoid inspecting the familiar landmark in favor of inspecting the newly learned landmark as soon as it was clear that the familiar tree did not provide food, as has been reported for chimpanzees in the wild (*67*). This kind of strategy would have been evident if we had found path linearity, once subjects had passed the disambiguation line, to clearly increase across trials and, similarly, if we had found angular deviation to decrease. However, we did not observe a clear trend. One subject (male Lobo) showed the hypothesized increase in path linearity across a few trials, while another (male Alex) showed high linearity from the first successful probe trial onward. However, others preferred to travel to the original landmark first.

These individual differences can be related to field data in different ways. Some chimpanzee individuals preferred to walk a familiar route first along their way toward the new food source. This could be akin to the situation of wild chimpanzees with limited relevant experience, for example, young females who newly enter a territory and are not yet familiar with its layout and phenology. In such cases, some individuals may be less risk prone and prefer to stick to familiar paths because taking new shortcuts and creating new travel paths create risks of losing your way. Humans traditionally use familiar routes to navigate instead of coordinate or vector maps that enable them to take shortcuts (*27*, *75*). Chimpanzees can be similar creatures of habit: For example, one study found those who return to last year feeding trees to monitor them to be more likely to monitor more familiar trees that they fed on most often in the past, irrespective of their quality or how many fruits they produced in the past (*7*). On the other hand, chimpanzees that live in open vegetation landscapes with which they are very familiar use few paths repeatedly within and especially across years and are capable of approaching food sources from many different directions (*30*). Alex's flexible behavior in the new location test was more reminiscent of these latter reports.

Our second aim was to relate the chimpanzees' responses in the virtual environment to those described in the wild using analytical techniques previously developed for analyzing GPS data. Across later stages of phase 1, as the chimpanzees were gradually learning to locate and approach the northern tree as the food location, their travel linearity in successful trials varied substantially, with median linearity across trials ranging from 0.58 to 0.88 between subjects. For comparison, a study of wild chimpanzees found the linearity of trajectories to out-of-sight food sources to be 0.85 on average in areas that were off familiar trails (*23*). At this point, it would be too early for drawing conclusions about common underlying cognitive processes. Factors that might affect the linearity of goal-directed travel, in virtual environments and real life, may include the general familiarity of the subject with the area, the number of times they have experienced food at the goal location, the distinctness of the goal location, or how often they have traveled a specific route. The more we establish that relationships between certain factors and linearity apply in similar ways in virtual reality and real life, the more it becomes plausible that inferences about those variables that can more easily be measured in VR (e.g., the exact number of times food was encountered in a specific location) may also be drawn for real-life spatial cognition.

One of our main questions with regard to path efficiency was whether subjects would show increases in linearity and decreases in angular deviation over time for paths that are traveled repeatedly. Regarding linearity, tentative evidence for efficient path taking came from the analysis of trials of type 1C, considered together, across phases 1 and 4 (result 4). Three of the six subjects showed clear increases in linearity, while two showed nonsignificant linearity increases. However, another subject (female Dorien) showed a significant decrease in linearity, performing more poorly in some of the later type 1C trials, that is, those trials that were intermixed with trials in which food was hidden in the new location. Other analyses of performance over time failed to find any linearity increases. First, in the later stages of phase 1, that is, stages 1B+, 1B++, and 1C in which the goal tree but not the fruit was visible, we did not find linearities to increase significantly. One reason may be our adaptive test design: The sudden increase in walking distance that comes with each promotion may have offset linearity increases that could have otherwise been observed had the subject been allowed to continue on their current stage. That linearity increases were indeed found for a number of chimpanzees when considering a larger number of identical trials (type 1C trials, result 4) supports this speculation. Second, across successful no-hint probe trials of phase 4, only one individual exhibited an increase in linearity toward the new goal location. Again, one reason may be that the number of trials was too small to observe subtle increases. In addition, several subjects appeared to settle early on a strategy of using the old landmark as a beacon, which they approached first and from which they then went on to discover the fruit hidden behind the new landmark. While consistently leading them to success, this may have stalled increases in linearity that would have resulted from exploring shorter routes to the new goal.

Regarding angular deviation, evidence was similarly inconclusive and mirrored the results for linearity in large parts. The best evidence for a decrease in angular deviation, that is, an improvement

by subjects in approximating the optimal route at trial start, came from the analysis of a larger number of identical trials (type 1C trials): For two subjects, there was a significant negative effect, such that angular deviation was smaller in later trials. In the analysis of later trials of phase 1 (that is, stages 1B+, 1B++, and 1C, when only the tree, but not the food, was visible), angular deviation fluctuated substantially for several subjects and did not show clear decreases over time. As for the analysis of linearity, it is possible that clearer evidence of decreasing angular deviation may have been obtained had each subject been allowed to practice trials of a given type beyond initial successes. Similarly, the relatively small total number of successful trials in phase 4 may explain why no interaction effect was found that would support the hypothesis that subjects learn over time to shortcut toward goal 2 as soon as they see that goal 1 is empty. In addition, the optimal routes from the disambiguation line to the old goal and to the new goal often lay quite close together (see, e.g., the trajectories by male Alex in Fig. 8B, bottom), with only a small angle between them. This may have made it more difficult to detect a subtle difference in heading toward the new goal in probe versus baseline trials.

Of course, this contrast between improvements in simple success rates and a lack of clear, initial improvement regarding linearity or angular deviation can be informative on its own (e.g., in the context of alternative routes taken in phase 4). That said, to improve the usefulness of GPS-style movement data further as valid measures of path efficiency, we recommend (i) that future studies allow for additional trials beyond initial success so that further efficiency improvements could be found, (ii) that costs associated with inefficient routes are sufficiently high (e.g., time spent and risk of losing food), and (iii) that the angle between efficient and inefficient hypothetical trajectories is sufficiently large even when close to the starting point to discover differences in initial walking direction.

In summary, our results illustrate how virtual environments can help in studying spatial cognition in novel ways. First, they allow for an in-depth study of spatial learning through repetition. By observing how individual travel routes evolve across repeated occasions of traveling from one location to another, we managed to collect tentative evidence of route linearity gradually improving over time (type 1C trials, although this was shown more strongly in some subjects than in others, as suspected). It is often assumed that such repeated visits to key locations are one way in which primates learn to travel efficiently, but in the wild, this effect can rarely be demonstrated because the individual's learning history is not known and/or because individuals often travel in groups. Second, presenting multiple subjects with the same virtual environment can reveal important individual differences in problem-solving, e.g., the use of different strategies by successful subjects in the no-hint probe trials of phase 4. Last, phase 3 showed that virtual environments make it possible to effectively run translocation tests with chimpanzees and that, at least in this experiment, the chimpanzees were able to pass these tests. In real life, translocation tests are typically restricted to insects or certain fish or bird species but are usually impractical with great ape species, and acquiring data that are equally informative (e.g., observing individuals navigating toward the same goal from different directions on different days) can be very time-consuming and dependent on luck.

Navigation experiments with virtual environments harbor great potential to contribute to old and new debates in spatial cognition. This includes the use of Euclidean versus route-based maps (*10*, *30*), the relative contributions of path integration versus landmark use (*51*), egocentric versus allocentric perspective taking (*39*), sensitivity to temporal variation (*7*, *67*), and metacognitive monitoring of spatial knowledge (*52*). In addition, we hope that in this context, new methods can be developed for analyzing, modeling, and predicting walking paths that are inspired by and may, in turn, inspire observational research in spatial cognition (*13*, *22*).

While the extension of virtual environments to other taxa and research question holds much promise, we need to acknowledge limitations and open questions with regard to the comparability of real-life and virtual navigation. First, we need further cross-validation of real-life and virtual navigation behaviors (e.g., shortcutting, detouring, and latent learning) to establish that subjects, above and beyond approaching objects that they associate with reward, regard the virtual environment as space in which they can move, explore, and identify objects with which they can interact. For example, the physical constraints on translational and rotational movement in digital versus real-world spaces are very different. The nature of these constraints and their effects on animals' paths of responding should be studied. Second, researchers of human navigation have pointed out that navigation in virtual environments does not afford a range of idiothetic and proprioceptive navigation cues, which may explain why humans more easily feel lost and disoriented in desktop virtual environments than in real ones (*51*–*53*). These concerns likely apply to the testing of nonhuman animals as well. In addition, many animals, including primates, use auditory and olfactory information when navigating, cues that were largely missing in the present study. While some of these problems will certainly be addressed as even more immersive virtual reality technologies become available for nonhuman animals, they need to be carefully considered, for example, when designing experiments to study latent learning and shortcut taking. Last, many animals, including many primate species, travel in groups in the wild. Joint travel involves social-cognitive processing of information that goes beyond individual spatial-perceptual and memory processes, e.g., following another individual or a majority of individuals, the social learning of routes, or communicating the presence of resources or the intention to depart (*21*, *76*, *77*). What the present study has in common with many real-life experiments of spatial cognition in captive primates is that all subjects were tested individually. Future studies in virtual environments that focus on the social aspect of navigation should complement studies of purely individual navigation.

Virtual environments are likely to prove useful in studying spatial cognition not only in chimpanzees but also in other primate species and other animal taxa. For example, in pilot studies, four bonobos at the Ape Cognition and Conservation Initiative and three orangutans at Leipzig Zoo learned the APExplorer gameplay mechanics at similar speeds as the chimpanzees in the current study. More generally, virtual environments may be used for studying navigation in any species that can use an input device like a touch screen, eye tracker, or joystick for computerized testing with visual feedback. The list of species that have successfully been trained for computerized testing currently includes all great ape species (*Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*, and *Pongo* spp.), capuchins (*Sapajus apella*), macaques (*Macaca* spp.), dogs (*Canis familiaris*), kea (*Nestor notabilis*), pigeons (Columbidae spp.), and bottlenose dolphins [*Tursiops truncatus*; see (*61*, *71*, *78*–*80*)]. Moreover, with virtual environments, there is no need to restrict studies to investigating ground navigation; rather, environments could be tailored to the study species, e.g., with flight simulation for avian species. In the

study of navigation of homing pigeons, for example, this would not only eliminate the costs of releasing and retrieving study animals but would also allow for levels of experimental control that are impossible to achieve in real-life experiments (e.g., including versus excluding large landscape features like rivers or mountain ranges). In addition to studying one species' spatial cognition in an environment tailored to their needs, virtual environments can also be used to ask the complementary question: How do two species with different feeding ecologies compare in navigating an identical environment that has specific foraging affordances? Last, the study of cognition in virtual environments is not limited to the spatial domain. For example, introducing conspecific avatars in an individual's virtual environment (whose movements may be controlled by artificial intelligence or another individual) would allow one to study aspects of animal social cognition that have traditionally been studied with limited ecological validity in computerized testing (e.g., abstract games from behavioral economics). Aspects of social cognition that may be studied with virtual environments could include social learning, competition over resources, sharing of information, or spatial coordination in group hunting.

In conclusion, our study illustrates that noninvasive experiments in open-space virtual environments have great potential for primate spatial cognition. Chimpanzees in our study learned the basic game mechanics quickly and soon exhibited learning and decision-making patterns that resembled real-life navigation. They learned to recognize certain objects as landmarks and to orient and search for these when they could not see them. They flexibly adapted when food availability became less predictable. When they had found routes that worked, their walking trajectories were often consistent (and sometimes showed further gradual improvement). Provided that future studies can replicate and extend these findings to other species, virtual reality may prove to become a powerful tool to address longstanding questions in the evolution and development of animal navigation that had previously been difficult to study in captive environments and in the wild.

SUPPLEMENTARY MATERIALS

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View/request a protocol for this paper from *Bio-protocol*.

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Chimpanzees (*Pan troglodytes*) navigate to find hidden fruit in a virtual environment

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