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Chimpanzee Turning Behavior During Spatial Navigation in Virtual Environments

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Abstract – Primate spatial navigation is difficult to study in the wild due to limited knowledge of explanatory variables, and in captivity due to limited physical space. Presenting tasks in computer-generated virtual environments (VE) can overcome these constraints, providing precise location and timing data in completely configurable environments of any size. Here, we used VE to closely examine turning, a fundamental navigational behavior, to better understand whether chimpanzees make the shortest turn (<180°) to targets outside their field of view (FOV). We also examined how this behavior changed with experience in VE. Chimpanzees completed a first-person virtual food collecting task on a touchscreen involving two virtual foods, both initially visible on the screen, which they could approach and "collect" to receive a real food reward. Due to the first-person viewpoint in the VE, as they approached one food, the other food disappeared from the FOV depicted on the screen. We found limited efficient turning to the second food during early experience with VE and more efficient turning during later experience with VE, suggesting that this behavior develops over time. Although for most chimpanzees, efficient turning was accompanied by biases in food side choice and turn direction, they nevertheless also turned efficiently even when they went against those biases. We found individual differences in food side choice and turn direction over time, indicating no consistent progression of these turning behaviors in VE across individuals, but some within-individual consistency across tasks. By closely studying primate navigation behavior in VE, we can better understand how they perceive these environments, informing the design of future VE-based studies.

Keywords – Object permanence, Turning behavior, Spatial cognition, Navigation, Virtual environment, Primates

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Studying spatial navigation in primates presents many challenges. In the wild, primate movements can be observed in their full socio-ecological context, but it is difficult to quantify variables like terrain type and the relative locations of individuals and food, making it hard to tease out how different factors affect navigation. Additionally, experimental manipulations in the real world are limited to providing baited feeding sites at particular locations (Bicca-Marques & Garber, 2004; Garber & Dolins, 1996; Garber & Paciulli, 1997; Janson, 1998, 2007; Teichroeb, 2015; Teichroeb & Aguado, 2016). Studies with captive primates overcome some of the limitations of field studies but have drawbacks of their own. Conducting studies in captive primates' enclosures enables greater control over the environment than in the wild, allowing for more precise experimental manipulations and easier collection of location and behavior data for all individuals in the group (Gibeault & MacDonald, 2000; MacDonald, 1994; MacDonald & Agnes, 1999; Mendes & Call, 2014; Menzel, 1973). However, these studies necessarily occur on a much smaller scale than field studies and are also limited in terms of the manipulability of terrain and environmental features, as well as the ecological validity of their findings.

Computerized tasks allow for tight control over the environment, including size, terrain type, the location of "food" (or targets for which the subject is rewarded) and environmental complexity (e.g., trees, rocks, etc.), and the starting location of the subject. It is also possible to collect data on the precise location of the subject and what is in their field of view (FOV) multiple times per second, enabling fine-grained analyses of subject movement and scanning behavior. Early computerized studies examined primates' abilities to navigate two-dimensional (2D) mazes from an overhead viewpoint using a joystick (Beran et al., 2015; Fragaszy et al., 2003; Mushiake et al., 2001; Washburn, 1992). Recent technological advancements have made the use of computer-generated three-dimensional (3D) spaces feasible for primate cognition research (Allritz et al., 2022; Dolins et al., 2014, 2017). Subjects can be presented with a first-person viewpoint of these virtual environments (VE), which responds to their self-directed "movement" throughout the virtual space via joystick or touchscreen, more closely mimicking their experience navigating physical environments. One benefit of using VE to study primate cognition is the ability to present tasks in larger and more varied environments than the physical environment available in most captive settings, for example, tasks that investigate memory for foraging locations spread over large areas. VE can also be used to present potentially more naturalistic tasks that would otherwise be impossible in captive settings due to physical or ethical constraints, such as tasks that examine hunting behavior. And unlike field studies, all variables in VE can be tightly controlled and the precise location and FOV of the subject in the environment can be recorded.

Prior primate cognition studies using less-immersive desktop-based VE (compared to more-immersive VE using a head-mounted display) have largely investigated navigation, examining how efficiently subjects move to targets in the environment and whether they are able to use landmarks to find targets (Allritz et al., 2022; Dolins et al., 2014, 2017; Sato et al., 2004; Washburn & Astur, 2003). Rhesus macaques (*Macaca mulatta*) learned to navigate to targets in virtual 3D mazes, even when the targets were located in novel locations, and their search behavior was both efficient and similar to that seen during navigation of virtual 2D mazes (Washburn & Astur, 2003). Japanese macaques (*Macaca fuscata*) learned to navigate to a target location in a virtual building from various starting positions (Sato et al., 2004). Chimpanzees (*Pan troglodytes*) and a bonobo (*Pan paniscus*) could use landmarks to navigate to targets in virtual mazes, with performance comparable to that of humans (Dolins et al., 2014, 2017). Finally, chimpanzees could efficiently locate targets in an open, semi-naturalistic VE using a landmark, even from novel starting positions, and navigate toward a different landmark when the target changed location (Allritz et al., 2022).

Using less-immersive VE to study spatial cognition has thus shown great promise, but how navigation behavior in VE develops over time remains unstudied. Chimpanzees have successfully completed navigation tasks in an open, semi-naturalistic VE within a remarkably short amount of time (fewer than 60 trials; Allritz et al., 2022), particularly compared to some 2D computerized tasks that take thousands of trials to learn (Allritz et al., 2016, 2021; Ohshiba, 1997; Tomonaga et al., 1993). By closely examining chimpanzees' behavior in VE over time, we can better understand the developmental trajectory of these behaviors. Do chimpanzees navigate efficiently from the start, suggesting that they may automatically bring their real-world experience to bear in VE tasks? Does navigation behavior change with experience in VE, suggesting learning or a refinement of navigational strategy? And what is the variation in navigation behavior between individuals?

Answering these questions is critically important for gauging how primates' perception of VE compare to their perceptions of the real world. VE do provide some of the same cues to three-dimensionality that we experience in the actual world, including linear perspective, pictorial depth cues, and the occlusion of objects, which change with the location and perspective of the subject in the environment (Dolins et al., 2017). However, less-immersive VE lacks the important depth cues of parallax and stereopsis, as well as proprioceptive and vestibular input when moving through the space, which have been found to aid in spatial navigation (Ruddle et al., 2011; Ruddle & Lessels, 2009). Additionally, the FOV is greatly reduced, and this view must be shifted by interacting with a touchscreen or joystick, rather than moving the head or the eyes (Dolins et al., 2017). In order to draw meaningful conclusions from VE studies, it is important to determine whether primates perceive VE as representations of 3D space and treat them accordingly.

Despite the lack of some depth and vestibular cues in less-immersive VE, similarities in spatial cognitive abilities in real environments and less-immersive VE have previously been found in humans. Not only do humans perform comparably on some (though not all) types of navigation and route-learning tasks in less-immersive VE and real environments (Coutrot et al., 2019; van der Ham et al., 2015), they also show similar patterns of learning and individual differences (Weisberg et al., 2014). There are also some similarities in gaze behavior in less-immersive VE and the real world (Dong et al., 2020). VE-based navigation tasks can even be used to diagnose spatial memory impairment (Cushman & Duffy, 2008; Hort et al., 2007; Weniger et al., 2011). Additionally, practice navigating in a virtual version of a space can later aid in navigating the actual space (Waller et al., 1998). These similarities suggest that there are some ways in which humans treat less-immersive VE as they do real environments, so it is not unreasonable to expect that other primates may do the same.

Chimpanzees have demonstrated some behaviors that suggest that they treat VE like 3D space. In one study, chimpanzees learned to navigate toward virtual fruit in a location that was visible at first, but then was no longer in the FOV as the subject's starting location was moved further and further away (Allritz et al., 2022). When the starting point was changed to a novel location in the VE, the chimpanzees could still navigate to the initially out-of-view fruit. Importantly, their success on these novel starting point trials could not be explained by their merely learning to make a series of taps to particular locations on the touchscreen; they had to find a new path to the fruit. Additionally, when the chimpanzees navigated to the fruit from the same starting location in multiple trials, some individuals took relatively direct routes, with increasing path linearity across trials. These results indicate that the chimpanzees understood that objects existed in the VE and could navigate toward them even when they were not in the FOV, providing some evidence for the chimpanzees treating VE like 3D space.

However, the chimpanzees only completed a maximum of 24 trials of the same type, providing a small developmental window into a complex behavior (Allritz et al., 2022). Here, we analyzed a simple navigation behavior (turning) in two tasks that took place at different points in chimpanzees' VE experience, enabling us to examine the developmental trajectory of this behavior more closely. Although turning is a very simple navigational behavior, it may be foundational for building more complex navigational skills. On a large scale, changes of direction in travel routes, often operationalized as change-points (Byrne et al., 2009), serve as important decision-making points during navigation (Garber, 2000; Janmaat et al., 2021). These locations are frequently associated with high-value food sources (Asensio et al., 2011; Ban et al., 2016; Janmaat et al., 2013a; Joly & Zimmermann, 2011) or greater visibility of landmarks or the home range (Garber & Dolins, 2010; Noser & Byrne, 2014; Presotto et al., 2018), enabling more efficient navigation. The ultimate target may have been last seen days or weeks before, or inferred based on other cues (Janmaat et al., 2013b; Menzel, 1991). We used fine-grained location and perceptual VE data to examine turning behavior on a smaller scale of distance and time, exploring the following questions: When a previously visible target is no longer in the primate's FOV, can they turn and move toward it, indicating that they know that target is still in the environment? When navigating toward a target out of their FOV, do they take the shortest path, suggesting they know the target's approximate location? How does turning behavior change with VE experience, and how consistent is this between individuals?

We investigated these questions by assessing the turning efficiency of chimpanzees navigating to an out-of-view target in a VE depicted on a touchscreen. We examined turning behavior in two tasks, one conducted early in the chimpanzees' VE experience and one conducted later, which both incorporated the following scenario: there were two virtual fruits, both initially visible on the screen, which the chimpanzees could approach and "collect" to receive an actual piece of that type of fruit as a reward. Due to the first-person viewpoint in the VE, as the chimpanzee approached one fruit, the other fruit disappeared from the FOV depicted on the screen. We examined whether chimpanzees made the efficient turn (<180°) to this now not-visible second fruit. If the chimpanzees immediately turned toward the second fruit, rather than going elsewhere in the environment, that would indicate that they have object permanence for objects in virtual space, as they do for objects in the real world (e.g., Barth & Call, 2006). Moreover, turning efficiently toward the second fruit would suggest that they knew its approximate location even though it was out of immediate sight. We also investigated whether turning behavior changed over time, as the chimpanzees may have developed strategies as they became more familiar with the VE. By closely examining turning behavior in VE, we can begin to understand whether primates perceive VE as representations of 3D space, which would have implications for the use and design of VE-based tasks in future studies.

Method

Ethics Statement

Research was approved by the Wolfgang Köhler Primate Research Centre (WKPRC) committee composed of the director of WKPRC, the research coordinator, the head keeper of great ape husbandry, and the zoo veterinarian. All research and husbandry complied with the European Association of Zoos and Aquaria (EAZA) and the World Association of Zoos and Aquariums (WAZA) regulations. Participation was entirely voluntary and non-invasive, and subjects were never food or water deprived. Water was available *ad libitum* both in the apes' enclosures and testing rooms.

Subjects

Six chimpanzees (three females; age *M* = 26.17 years old, *SD* = 15.55) participated in the Quality Preference (QP) task (Table 1). Six chimpanzees (three females; age *M* = 29.67 years old, *SD* = 14.05) participated in the Four Valleys (FV) task; five of these chimpanzees had also participated in the QP task. All chimpanzees had prior touchscreen experience with tasks involving static or moving stimuli (e.g., Allritz et al., 2016, 2021; Voinov et al., 2020) and prior experience with VE presented on touchscreens (Table 1 and detailed below).

The chimpanzees were housed at the WKPRC in Leipzig Zoo, Germany. All chimpanzees lived in a social setting with access to climbing structures, foraging boxes, and seasonal access to outdoor enclosures. On each testing day, subjects were able to enter a testing room and participate in cognitive tasks to earn food rewards additional to their regular diet.

Table 1

Chimpanzee Demographic Information and Prior VE Experience

Subject	Sex	Rearing history	Age during QP Task	VE experience prior to QP Task	Age during FV Task	VE experience between QP and FV Tasks
Alex	M	Hand	16	Training	18	Memory Task Pilot Navigation Task [a] + additional stage
Bangolo	M	Parent	8	Training	--	Did not participate in FV Task
Dorien	F	Hand	36	Training	39	Navigation Task [a]
Fraukje	F	Hand	41	Training	43	Navigation Task [a]
Frederike	F	Unknown	43	Training	45	Navigation Task [a]
Lobo	M	Parent	13	Training	15	Navigation Task [a]
Lome	M	Parent	--	Did not participate in QP Task	18	Training Navigation Task [a]

Note. [a] *Allritz et al. (2022)*

Apparatus and Software

Tasks were presented on a Viewsonic 19" computer monitor (aspect ratio 5:4, resolution 1280 x 1024 pixels) placed behind an infrared touchscreen panel that was located at around chimpanzee face height in the testing room. Subjects interacted with a sheet of transparent polycarbonate located in front of the monitor, which would relay the location of their touches to the computer and change the FOV in the VE accordingly.

The VE tasks were run on a Windows PC using the APExplorer 3D app (Schweller et al., 2022) which was programmed in C# using the Unity3D game engine. For a more detailed description of the apparatus and software, see Allritz et al. (2022).

Tasks

The data in this paper came from two tasks originally designed for purposes other than examining turning efficiency. However, both tasks contained trials where there were two virtual food items located in front of the subject in a semi-naturalistic VE such that when the subject approached one food item, the other food item disappeared from the FOV depicted on the touchscreen. The subjects received a food reward for "collecting" each virtual food item by approaching it in the environment. When the subject moved close enough to the virtual food, it briefly vibrated or rose up before disappearing, while a "ta-daa" sound played. The subject was then given a piece of the corresponding food as a reward (i.e., rewarded with a piece of apple for collecting a virtual apple, etc.). The tasks took place in two different VE with the same aesthetic and a similar design. Both VE were bounded by a continuous high stone wall, had a blue sky with white clouds, and had a ground resembling grass and/or dirt. Both VE also contained natural 3D-rendered elements such as bushes, trees, rocks, and flowers. Subjects could move around and turn in the VE by touching the touchscreen. When the screen was touched, the subject would move to that location in the VE, turning to orient to that location if needed. If there was an impermeable virtual object, such as a rock or a wall, in the path to the touched location, their movement would stop at that impermeable object. Subjects could turn in place (that is, rotate without moving forward) by touching in the bottom left and bottom right corners of the screen. Touches to the area of the screen depicting sky yielded no movement. (For a more detailed description of movement in the VE, see Allritz et al. [2022]). For each trial, the VE program output a data file containing trial type information (including the type and location of each food item), the location of the subject in the VE every 500ms, and the timing of every food item collected. Each trial was initiated by the subject by touching a black-outlined white square on the touchscreen. All sessions were video recorded from behind the subject, so the subject's interactions with the touchscreen could be seen.

Prior to participating in the tasks analyzed here, all chimpanzees participated in a training program designed to teach them how to move around the environment via the touchscreen, navigate around obstacles such as rocks and trees, and approach virtual food items to receive a reward (McEwen et al., 2025). Training took place in a square-shaped arena containing trees, rocks, bushes, a pond, and virtual food. At the beginning of the training program, the virtual food was located near the subject's starting position, enabling them to receive a reward within a few touches of the touchscreen. As the training progressed, the food was moved farther from the subject's starting position, requiring them to interact with the touchscreen more and become more precise in their navigation to receive a reward. Subjects also received help from the experimenter during the early stages of training; this help consisted of the experimenter navigating around obstacles if the subject got stuck or redirecting the subject toward food if they moved far away from it. The amount of help from the experimenter decreased as subjects progressed through training until they received little to no help by the end of training. Subjects completed between six and nine of these training trials.

Quality Preference (QP) Task

The QP task was conducted between May and August 2017. Prior to this task, the chimpanzees had only experienced a VE on a touchscreen through the training program described above. The purpose of the QP task was to gauge the chimpanzees' preferences for different food item rewards associated with their corresponding virtual food items in the environment. Another condition of the task, which was not analyzed here, assessed the chimpanzees' preferences for one food item versus three food items in the VE. Sessions of these two conditions were given alternately, and were interspersed with non-VE sessions where the chimpanzees could choose between pieces of two different actual foods and between one piece and three pieces of actual food (also not analyzed here). The VE was the same arena used in VE training, with just two different food items located in front of the subject's starting position and in their FOV, one on the left and one on the right (Figure 1A, Video S1). The arena also contained trees, bushes, and rocks, but none of these items were located near or in between the two food items and the subject. The food items used in the arena were apples, bananas, and grapes. The two types of food items presented in each trial were randomized and the side that each type of food item was on was counterbalanced. If the subject did not collect both food items within 60 seconds, that trial ended and the start screen for the next trial appeared. Each subject completed six sessions of 12 trials, for a total of 72 trials each. Subjects were given one session each day and incomplete sessions were finished the next testing day. Sessions were terminated early if a subject did not interact with the touchscreen for approximately four minutes, showed no interest in food rewards, or showed signs of fear or distress (which happened rarely). Data files for three sessions (one session for each of three subjects) were lost; some data were therefore obtained by coding videos from those sessions, as described below.

Four Valleys (FV) Task

The FV task was conducted between April and November 2019. Between the QP task and the FV task, the chimpanzees completed a navigation task in the same VE as VE training and the QP Task but with additional rocks, bushes, and short walls (Allritz et al. 2022). This task investigated whether subjects could learn to navigate to a landmark with virtual food from various starting locations, and navigate to a new landmark when the food was no longer at the previous landmark. One chimpanzee (Alex) completed an additional intermediate stage of the navigation task that was not done by the other chimpanzees, consisting of six trials that involved finding virtual food in novel locations, interspersed with seven trials from a previous experimental stage. All chimpanzees were able to use a landmark to navigate to food that was not directly visible from their starting location from various distances and starting locations, although there were large individual differences in path linearity and the ability to navigate to a new landmark (Table S1). Alex also participated in 40 trials of a pilot memory study immediately after the QP task, which took place in the QP VE and investigated whether he could remember the locations of hidden virtual food. Neither of these intervening studies included trials with the same relative location of two food items and subject as are analyzed here. One chimpanzee (Lome) did not participate in the QP task but completed the VE training program and the navigation task prior to the FV task. One chimpanzee (Bangolo) who completed the QP task did not participate in the FV task.

The VE used in the FV task was octagonal, with two long ridges arranged in an "X" shape quadrisecting the environment, creating four roughly triangle-shaped valleys (Figure 1B). The ridges were high enough that when the subject was in a valley, the other valleys were not visible, but multiple valleys could be seen at once from the top of the ridges. To differentiate the valleys from each other, each valley had a different color ground (sand, yellow, green, or brown) and contained a different arrangement of rocks and trees in the area near the boundary wall of the VE. Partway through the Double phase of the task (details below), trees and flowers were added to the perimeter of the arena and the top of the ridges for all chimpanzees except Alex, to encourage the chimpanzees to explore the arena. The purpose of the FV task was to examine whether the chimpanzees could take the shortest route between virtual food items (apples, bananas, grapes, or peanuts) placed in different valleys. Valleys were baited with either two, five, or 10 of the same food items; we only examined trials where at least one valley was baited with two food items. A valley was always baited with all of the same type of food item (e.g., all apples), although if multiple valleys were baited in a trial, each valley was baited with a different type of food item (e.g., one valley was baited with apples and another valley was baited with peanuts). Food item types and baited valleys were randomized and counterbalanced across trials. Subjects were given one session each day and incomplete sessions were finished the next testing day. Sessions were terminated early if a subject did not interact with the touchscreen for approximately 4 min, showed no interest in food rewards, or showed signs of fear or distress (which happened rarely).

Each trial began with the subject starting in the center of the VE, on top of the intersection of the two ridges, facing one of the four valleys. The food items in a baited valley were located about halfway between the subject's starting position and the boundary wall of the VE. From the subject's starting perspective at the center of the VE, one food item was on the left and one food item was on the right.
The task consisted of three phases: Single, Double, and Horseshoe.

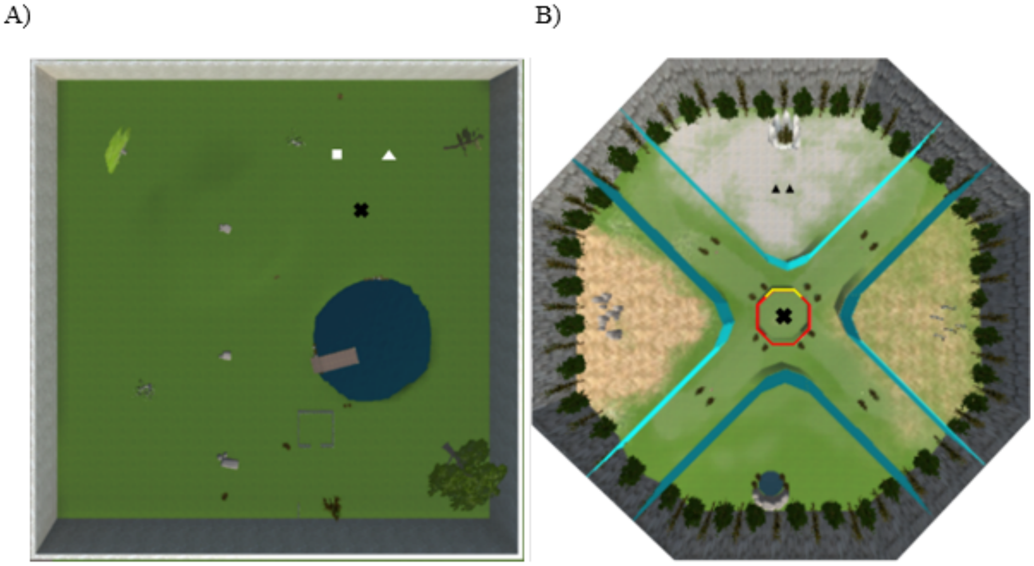
In the Single phase, only one valley was baited with two food items (Video S2). The trial began with the subject facing a valley, then turning 360 degrees clockwise or counterclockwise to get a view of all four valleys. During this spin, the subject was unable to move around in the VE. The spin ended with the subject facing the first valley again, and then movement around the environment was enabled. If the subject did not collect both food items within 100 seconds, that trial ended and the start screen for the next trial appeared. Each session consisted of eight trials, and subjects completed between three and seven sessions, for a total of 24-47 trials each. Due to motivation issues, two chimpanzees completed Single "Refresher" sessions after completing three Double sessions. These Refresher sessions are included in the Single phase trial counts and analyses.

In the Double phase, two valleys were each baited with two food items (Video S3). Each trial began as in the Single phase, with the subject spinning 360 degrees clockwise or counterclockwise before moving was enabled. If the subject did not collect all four food items within 100 seconds, that trial ended and the start screen for the next trial appeared. Each session consisted of between two and eight trials (not including trials where valleys contained five or 10 food items), and subjects completed between 11 and 20 sessions, for a total of 35-162 trials each.

In the horseshoe phase, two valleys were each baited with two food items (Video S4). Trials did not begin with the subject spinning to see all of the valleys. Instead, the subject began each trial facing one of the valleys and was allowed to move around the VE immediately. Access to all but one baited valley was blocked by an invisible barrier; they could only access the other valleys once they had entered the permitted baited valley. If the subject did not collect all four food items within 150 s, that trial ended and the start screen for the next trial appeared. Each session consisted of six trials (not including trials where valleys contained 10 food items), and subjects completed between seven and eight sessions, for a total of 23-34 trials each.

Figure 1

Overhead View of the Virtual Environment in Each Task



Note. A) VE used in QP task. The black “x” indicates the starting position of the subject on each trial, with the subject always facing north. The white triangle and square indicate the approximate location of the two food pieces on each trial. B) VE used in FV task. The blue lines (not visible during the task) indicate the boundaries of the ridges that delineate the four valleys, which have different ground colors and different landmarks near the perimeter wall. There are trees and bushes on top of the ridges and lining the perimeter wall, which were added partway through the Double phase for all chimpanzees except Alex. The black “x” indicates the starting position of the subject on each trial. The red line indicates where a subject would be blocked from moving at the beginning of a Horseshoe trial forcing them to enter the north valley, and the yellow line indicates where the subject would be allowed to move. The two black triangles in the north valley indicate the approximate location of the two food pieces in a valley.

Video Coding

Data that could not be extracted from APExplorer’s data files were obtained by coding video of the chimpanzees doing the tasks, using BORIS (Friard & Gamba, 2016). These data included the side of the first food item chosen (from the player’s perspective), whether the second food item was visible when the first food item was collected, the direction of the player’s turn after collecting the first food item, and whether the player left the touchscreen between collecting the first food item and turning. Three QP sessions with video but missing data files were also coded for whether the trial timed out before both food items were collected and how many food items were collected in the trial. The video for two FV sessions was corrupted; those trials were excluded from all analyses.

All trials were coded by the lead author (SK) according to the coding scheme in Table 2. 10% of trials were reliability coded by a second coder. Inter-rater reliability was strong for side of the first food item chosen (kappa = .90), visibility of the second food item when the first food item was collected (kappa = .95), and turn direction (kappa = .90). Inter-rater reliability was moderate for whether the chimpanzee left the touchscreen between collecting the first food item and turning (kappa = .74). The coding for whether a trial timed out before both food items were collected and how many food items were collected in the trial was identical for the two coders.

Table 2

Video Coding Scheme

Variable	Coding instructions
First food item choice	Which food item the player collected first, the one on the left (L) or the one on the right (R). These sides are player-centric and thus depend on the direction the player approaches the food item from. For example, say that from the player's starting position, the food item on the left is Food ItemA and the food item on the right is Food ItemB. If the player walked past the food item, turned around, and approached the food item from the opposite direction, Food ItemA is now on the right and Food ItemB is now on the left. If the player approached the food item from the side, so one food item appeared to be in front of the other, code it as "SIDE". If you can't see which food item was collected first (for example, if the chimpanzee's body was blocking the screen, or they turn around in the environment so much that you can't tell which food item they collect), code it as "UNCLEAR". (You likely won't be able to code the remaining variables for that pair of food item.)
Visibility of second food item	At the time that the first food item was collected (the food item rises and disappears, "ta-daa!" plays), was the 2nd food item (or its shadow) visible (1) or not (0)?
Leave touchscreen	After collecting the 1st food item and before making their 1st turn, did the player leave the touchscreen (1) or not (0)? The player is assumed to stay at the touchscreen unless they can be seen turning and moving away from the touchscreen and/or reapproaching the touchscreen from the side (rather than reappearing from the bottom as if they'd been crouching). A 2nd touch to the first food item does not count as a 1st turn (if a player touched the 1st food item a second time, then walked away, mark this as leaving the touchscreen). Also mark this as leaving the touchscreen if the player was not sitting at the touchscreen when the 1st food item was collected.
Turn direction	The direction that the player first turned after collecting the 1st food item (L or R). If the player touched the 1st food item again, this is the first turn after that touch. If the player moved straight ahead rather than turning (and was not just touching the 1st food item again), code the turn as "STRAIGHT". In cases where the player approached the food items from the side and didn't turn to collect the 2nd food item, code the turn as "STRAIGHT".
Timeout	Did the trial end before both food items were collected? Yes (1) or no (0).
Number of food items collected	How many food items were collected in the trial?

Analyses

In the Double and Horseshoe phases of the FV task, there were two pairs of food items that could be collected in each trial. For analysis purposes, the second pair of food items collected in a trial were treated as a separate trial occurring after the collection of the first pair of food items and before the actual next trial of the task. Two trials where the subject collected a food item from one pair, then collected a food item from the other pair were excluded. We excluded trials where the side of the first food item chosen could not be determined (QP $N = 0$; FV $N = 9$), the first food item was approached from the side (QP $N = 3$; FV $N = 11$), the second food item was visible at the time the first food item was collected (QP $N = 3$; FV $N = 55$), the trial ended before the chimpanzee turned after collecting the first food item (QP $N = 0$; FV $N = 18$), the chimpanzee went straight instead of turning after collecting the first food item (QP $N = 34$; FV $N = 34$), or the chimpanzee left the touchscreen between collecting the first food item and turning (QP $N = 7$; FV $N = 24$). There were no trials in either task where the turn direction was coded as unclear. In total, 43 QP trials (9.95%) and 112 FV trials (12.10%) were excluded, leaving a total of 389 QP trials (54-70 trials per chimpanzee) and 814 FV trials (82-279 trials per chimpanzee). We created a variable to indicate turning efficiency based on the food chosen and direction turned in each trial: if the subject either chose the food on the right and then turned left or chose the food on the left and then turned right, that trial was coded as efficient (1). If the subject either chose the food on the right and then turned right or chose the food on the left and then turned left, that trial was coded as inefficient (0).

We were interested in the behavior of the chimpanzees individually, so all analyses were conducted separately for each subject. Overall efficiency, first food item choice, and turn direction in each task were assessed using two-tailed exact binomial tests, as we wanted to detect whether subjects performed significantly above or below chance, which was set at 50%. Food item choice and turn direction were initially tested as the percentage of trials where the subject chose the right food item or turned right; if the result indicated that this occurred significantly less often than chance, the tests were re-run as the percentage of trials where the subject chose the left food item or turned left, for easier comprehension. Clopper-Pearson 95% Confidence Intervals were also calculated.

We investigated changes in efficiency, first food item choice, and turn direction over time in each task by regressing each of these variables separately on trial number using a generalized linear model with a logit link function and binomial error structure. Because turn direction could also be affected by the side of the first food item chosen – in fact, if a subject is intentionally turning efficiently, it should be – we included first food item choice along with trial number as predictors in that regression, as well as the interaction between food item choice and trial number. This enabled us to examine how first food item choice and turn direction were related across trials, for example, whether there was a learning effect wherein food choice and turn direction became more negatively related over time. If the interaction between food item choice and trial number was not significant, or the model with the interaction did not converge, the interaction was removed from the model to allow us to assess the relative effects of food item choice and trial number on turn direction. We used Firth's penalized maximum likelihood estimator (Firth, 1993), which has been shown to reduce bias and variance in smaller sample sizes (Rainey & McCaskey, 2021). Overall trial number was assigned after excluding trials where no fruit was collected but before excluding trials based on video coding or for which video was unavailable; thus, it accounts for all trials in which at least one piece of food was collected. Trial number within each task was scaled before being entered into the models. For food item choice and turn direction, "right" was coded as one, so the trial parameter estimate indicates an increase or decrease in choosing the right food item or turning right. Likelihood-ratio tests were used to assess the significance of predictors; if the effect was significant, then the odds ratio was calculated. We refit models that violated the assumption of linearity in the logit (i.e., the continuous predictor trial number was not linearly related to the logit) with restricted cubic splines (Schoenberg, 1946). When using splines, the relationship between a continuous predictor and the logit is characterized by a piecewise polynomial function. The continuous predictor is segmented and a polynomial function is fitted separately within each segment, with the constraint that the functions are continuous at the segment boundaries (called "knots"). Restricted cubic splines have the additional constraint that the first and last segments are linear, to better fit the data at the bounds of the predictor (Stone & Koo, 1985). The number of knots is specified by the user; to avoid overfitting, we fit each spline model with three, four, or five knots (yielding four, five, or six segments, respectively) and chose the model with the lowest AIC. In all cases, this was the model with three knots (df = 2), yielding a piecewise polynomial function made up of a linear function followed by two cubic polynomial functions and then another linear function. There was no multicollinearity in any multiple regression models.

For the FV task, we could not control for both trial number and task phase because they were confounded. Because there were some differences between the phases of the FV task (namely different numbers of baited valleys and free versus forced choice to one valley), we also conducted these analyses using phase (coded ordinally: Single, Double, Horseshoe) instead of trial number. The significance and direction of all results were the same regardless of whether trial number or phase was used, except for two regressions noted in Results. The results of these regressions are presented in Table S2.

Statistical analyses were conducted and figures were constructed in R v. 4.1.1 (R Core Team, 2021) using the tidyverse (v1.3.1; Wickham et al., 2019), broom (v1.0.5; Robinson et al., 2023), lme4 (v1.1.30; Bates et al., 2015), brglm2 (v0.9; Kosmidis & Firth, 2021), irr (v0.84.1; Gamer et al., 2019), ggplot2 (v3.4.0; Wickham, 2016), ggpattern (v1.0.1; FC et al., 2022), cowplot (v1.1.1; Wilke, 2020), logistf (v1.24.1; Heinze et al., 2022), and patchwork (v1.1.3; Pedersen, 2023) packages.

Results

Quality Preference Task

Overall Turning Behavior

Six chimpanzees completed this task, which was their first experience having two virtual foods located equidistant in front of their starting location. Four chimpanzees turned immediately after collecting the first food item in more than 95% of trials (Alex: 100%; Bangolo: 98.53%; Dorien: 98.51%; Fraukje: 97.22%). Frederike moved straight instead of turning after collecting the first food item on 25% of trials, and Lobo did so on 13.89% of trials. One chimpanzee turned efficiently significantly more often than chance (Fraukje), one chimpanzee turned efficiently significantly less often than chance (Frederike), and the remaining four chimpanzees did not turn efficiently more or less than chance (Table 3).

Table 3

Trial Number and Turning Efficiency for Each Chimpanzee and Task

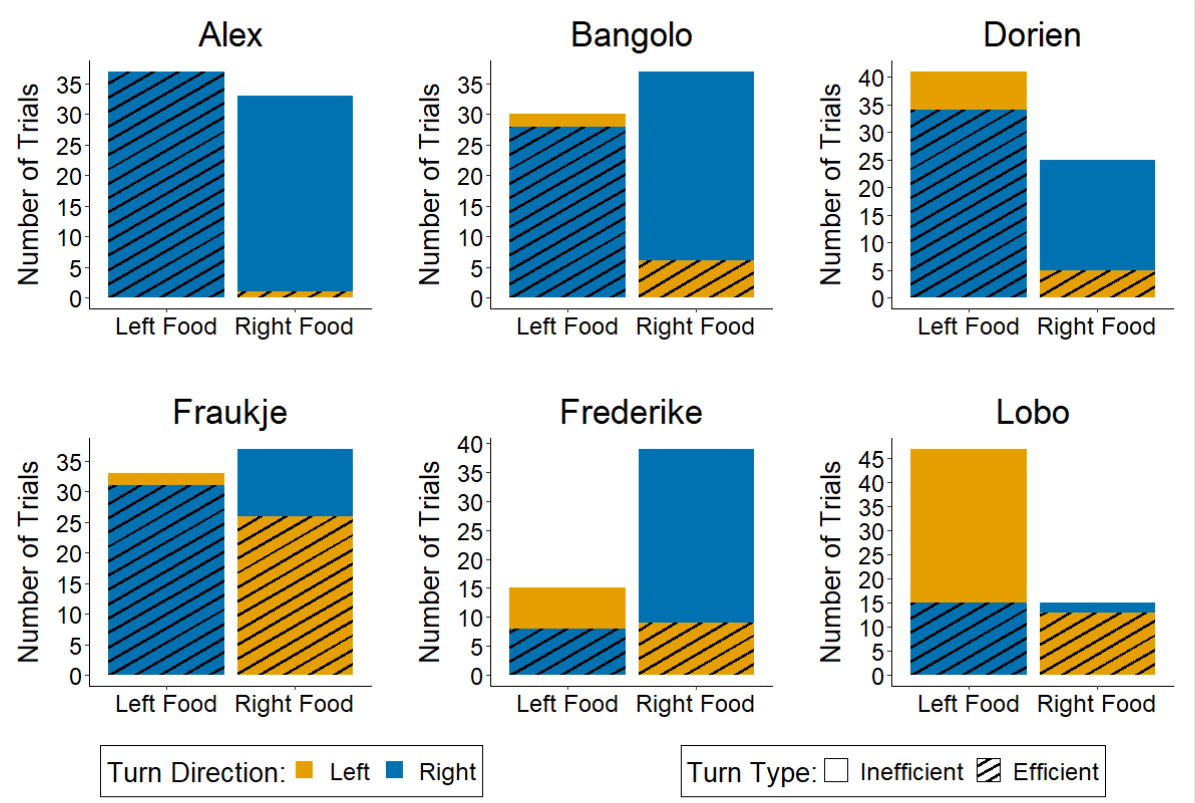
Subject	Quality Preference Task			Four Valleys Task		
	Trials (*N*)	Efficient turns	95% CI	279	94.98%**	[0.92, 0.97]
Alex	70	54.29%	[0.42, 0.66]	279	94.98%**	[0.92, 0.97]
Bangolo	67	50.75%	[0.38, 0.63]	--	--	--
Dorien	66	59.09%	[0.46, 0.71]	104	82.69%**	[0.74, 0.89]
Fraukje	70	81.43%**	[0.70, 0.90]	145	93.79%**	[0.89, 0.97]
Frederike	54	31.48%*	[0.20, 0.46]	115	33.04%**	[0.25, 0.42]
Lobo	62	45.16%	[0.32, 0.58]	82	93.90%**	[0.86, 0.98]
Lome	--	--	--	89	87.64%**	[0.79, 0.94]

Note. Clopper-Pearson 95% Confidence Intervals and significance were calculated from two-tailed exact binomial tests. *$p < .05$. **$p < .001$.

We next examined whether the chimpanzees' efficiency (or lack thereof) was due to any biases in the location of their first food item choice or in their turning direction. Efficient turning could be the result of sometimes choosing the left food item first and sometimes choosing the right food item first and turning in the efficient direction regardless (i.e., turning right when the left food item is chosen first and turning left when the right food item is chosen first). Or it could be due to a strategy of mostly (or always) choosing the food item on one side and mostly (or always) turning in the direction that is efficient for that food item side (i.e., mostly choosing the left food item first and then turning right *or* mostly choosing the right food item first and then turning left), whether intentionally or by chance. If the turn direction that is inefficient for that food item side is chosen instead, that would lead to inefficient turning. Randomly choosing the first food item side and turn direction would lead to turning that is not significantly efficient or inefficient.
Figure 2 shows the food item side choice and turning direction for each chimpanzee in the QP Task. The turning behavior of Alex, Bangolo, and Dorien, which was neither significantly efficient nor inefficient, was accompanied by an unbiased first food item choice and a significant bias to turn right (Table 4). Frederike turned significantly inefficiently and was significantly biased toward the food item on the right and to turn right. Lobo, who turned neither efficiently nor inefficiently, had a significant bias to choose the food item on the left and to turn left. Fraukje, the only chimpanzee in this task who turned significantly efficiently, was not biased in her first food item choice nor her turning direction.

Figure 2

Food Item Side Choice and Turning Direction in the QP Task



Note. The number of trials in which each food side was chosen first, by chimpanzee. Shading indicates subsequent turn direction; orange for left and blue for right. Diagonal lines indicate the food item choice and turn direction combinations that constitute an efficient turn.

Table 4

Percentage of Trials by First Food Item Choice and Turn Direction in the QP Task

Subject	Dependent variable	% of trials	95% CI
Alex	Right food item	47.14%	[0.35, 0.59]
	Turn right	98.57%**	[0.92, 1.00]
Bangolo	Right food item	55.22%	[0.43, 0.67]
	Turn right	88.06%**	[0.78, 0.95]
Dorien	Right food item	37.88%	[0.26, 0.51]
	Turn right	81.82%**	[0.70, 0.90]
Fraukje	Right food item	52.86%	[0.41, 0.65]
	Turn right	60.00%	[0.48, 0.72]
Frederike	Right food item	72.22%*	[0.58, 0.84]
	Turn right	70.37%*	[0.56, 0.82]
Lobo	Left food item	75.81%**	[0.63, 0.86]
	Turn left	72.58%**	[0.60, 0.83]

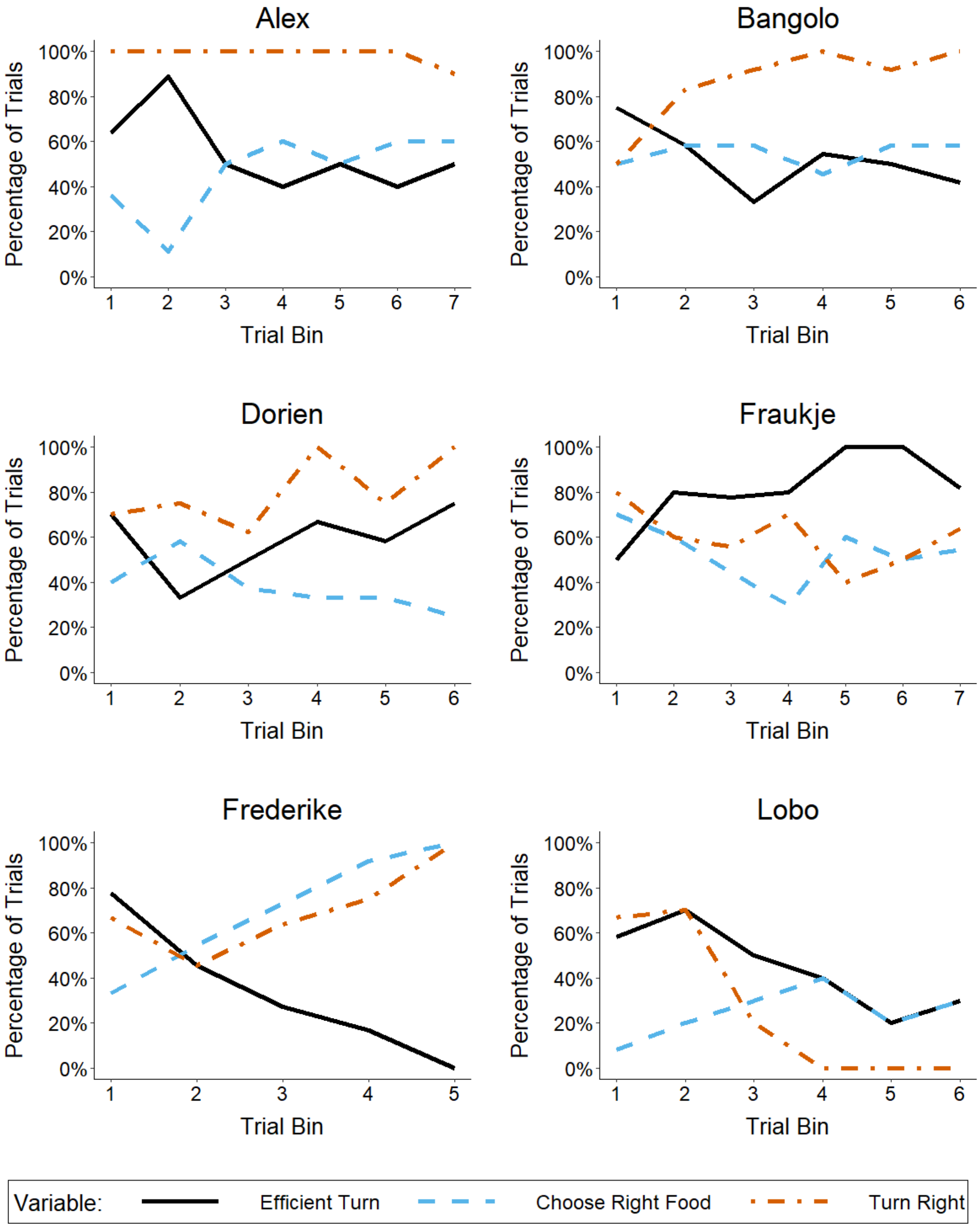
Note. Clopper-Pearson 95% Confidence Intervals and significance were calculated from two-tailed exact binomial tests. Food item choice and turn direction were initially tested as the percentage of trials where the subject chose the right food item or turned right; if the result indicated that this occurred significantly less often than chance, the tests were re-run as the percentage of trials where the subject chose the left food item or turned left, for easier comprehension. *$p < .05$. **$p < .001$.

Turning Behavior Across Trials

Figure 3 shows the chimpanzees' efficiency, food item choice, and turn direction behavior across trials. One chimpanzee's turning efficiency significantly increased across trials, two chimpanzees' efficiency significantly decreased across trials, and three chimpanzees' efficiency did not significantly change across trials. Alex turned right almost exclusively throughout the task, but his likelihood of choosing the food item on the right significantly increased across trials (Table 5). His turning efficiency did not change significantly over time. Bangolo maintained chance levels of efficiency and choosing the food item on the right throughout the task, while his likelihood of turning right significantly increased even when accounting for his choice of food item. None of Dorien's behavior changed significantly over time. Fraukje's efficiency significantly increased across trials. There was no significant change in her food item choice over time and she became less likely and then more likely to turn right across trials when accounting for her food item choice (Figure S1). Independent of trial number, Fraukje's food choice and turning direction were negatively related such that her likelihood of turning right was significantly lower when she chose the food on the right than when she chose the food on the left. Frederike's efficiency significantly decreased across trials, as her likelihood of choosing the food item on the right significantly increased. Her food choice and turning direction became more positively related across trials; she became more likely to turn right after choosing the food on the right over time. Lobo's efficiency significantly decreased across trials, as his likelihood of turning right significantly decreased when accounting for his food item choice, while his food item choice did not change significantly.

Figure 3

Efficiency, Food Item Choice, and Turn Direction across trials in the QP Task



Note. The percentage of trials in which chimpanzees turned efficiently (black solid line), chose the food item on the right first (blue dashed line), and turned right (red dot-dashed line) in the QP task, by chimpanzee. Trials are grouped in bins of 10-11 trials.

Table 5

Changes in Efficiency, Food Item Choice, and Turn Direction Across Trials in the QP Task

Subject	Dependent variable	Independent variable(s)	Likelihood ratio test			*B*	Odds ratio	95% CI
			X^2	*df*	*n*			
Alex	Efficiency	Trial #	2.84	1	70			
	Right food	Trial #	3.99*	1	70	0.48	1.61	[0.98, 2.64]
	Turn right [a]	Trial #	0.00	1	70			
		Right food	0.00	1	70			
Bangolo	Efficiency	Trial #	1.59	1	67			
	Right food	Trial #	0.07	1	67			
	Turn right [a]	Trial #	11.39**	1	67	1.45	4.28	[1.46, 12.54]
		Right food	1.77	1	67			
Dorien	Efficiency	Trial #	1.48	1	66			
	Right food	Trial #	2.07	1	66			
	Turn right [a]	Trial #	3.21	1	66			
		Right food	0.00	1	66			
Fraukje	Efficiency	Trial #	5.69	1	70	0.74	2.10	[1.07, 4.13]
	Right food	Trial #	0.42	1	70			
	Turn right [a]	Trial #	12.98*	2	70	-7.37 [b] 0.87 [c]	0.0006 2.39	[0.000004, 0.10] [0.02, 25.61]
		Right food	43.83**	1	70	-4.36	0.01	[0.002, 0.08]
Frederike	Efficiency	Trial #	16.25**	1	54	-1.34	0.26	[0.12, 0.59]
	Right food	Trial #	15.75**	1	54	1.37	3.95	[1.69, 9.22]
	Turn right	Trial # × Right food	8.71*	1	54	2.54	12.63	[1.44, 111.11]
Lobo	Efficiency	Trial #	4.89	1	62	-0.56	0.57	[0.33, 0.98]
	Right food	Trial #	1.37	1	62			
	Turn right [a]	Trial #	26.64**	1	62	-1.98	0.14	[0.05, 0.40]
		Right food	0.35	1	62			

Note. [a] The interaction between Trial # and Right food was not significant, so it was removed from this model. [b] Natural cubic spline one. [c] Natural cubic spline two. *$p < .05$. **$p < .001$.

Summary

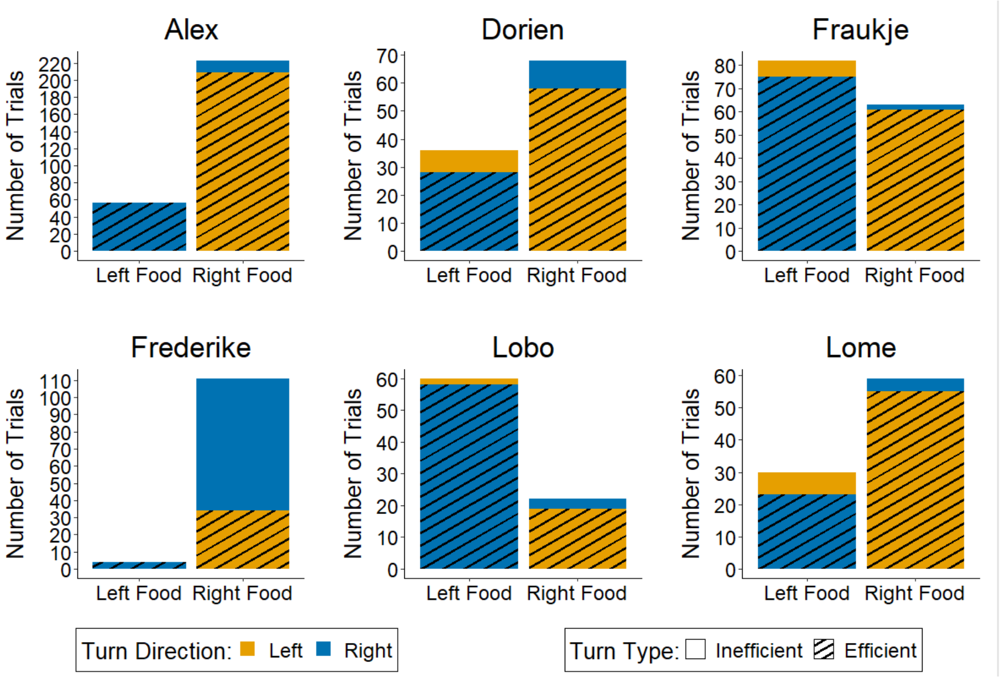
In the QP Task, one chimpanzee turned efficiently significantly more often than chance, one chimpanzee turned efficiently significantly less often than chance, and the remaining four chimpanzees did not turn efficiently more or less than chance. Five chimpanzees were biased in either their first food side choice, their turn direction, or both. The only chimpanzee without biases was also the only chimpanzee to turn efficiently. Across trials, one chimpanzee's turning efficiency significantly increased, two chimpanzees' efficiency significantly decreased, and three chimpanzees' efficiency did not change. Only the efficiently turning chimpanzee had a significant negative relationship between choosing the food on the right and turning right, independent of trial number. Two chimpanzees increasingly chose the food on the right, one chimpanzee increasingly turned right independent of his food choice, one chimpanzee increasingly turned right after choosing the food on the right, one chimpanzee decreasingly then increasingly turned right, and one chimpanzee increasingly turned left.

Overall Turning Behavior

Six chimpanzees completed this task, five of whom also completed the previous QP task, and all of whom completed a VE navigation task (Allritz et al., 2022). In the FV Task, all chimpanzees turned immediately after collecting the first food item in more than 95% of trials (Alex: 98.94%; Dorien: 98.11%; Fraukje: 97.32%; Frederike: 95.04%; Lobo: 95.35%; Lome: 100%). Five chimpanzees turned efficiently significantly more often than chance and one chimpanzee turned efficiently significantly less often than chance (Table 3). Figure 4 shows the food item side choice and turning direction for each chimpanzee in the FV Task. Alex, Dorien, and Lome, who all turned significantly efficiently, were all biased toward the food item on the right and to turning left (Table 6). Lobo's significantly efficient turning was the result of the opposite biases: choosing the food item on the left and turning right. Fraukje, the remaining chimpanzee to turn significantly efficiently, was not biased in her first food item choice nor her turning direction. Frederike's significantly inefficient turning was the result of biases toward the food item on the right and to turning right.

Figure 4

Food Item Side Choice and Turning Direction in the FV Task



Note. The number of trials in which each food side was chosen first, by chimpanzee. Shading indicates subsequent turn direction: orange for left and blue for right. Diagonal lines indicate the food item choice and turn direction combinations that constitute an efficient turn.

Table 6

Percentage of Trials by First Food Item Choice and Turn Direction in the FV Task

Subject	Dependent variable	% of Trials	95% CI
Alex	Right food item	79.93%**	[0.75, 0.84]
	Turn left	74.91%**	[0.69, 0.80]
Dorien	Right food item	65.38%*	[0.55, 0.74]
	Turn left	63.46%*	[0.53, 0.73]
Fraukje	Right food item	43.45%	[0.35, 0.52]
	Turn right	53.10%	[0.45, 0.61]
Frederike	Right food item	96.52%**	[0.91, 0.99]
	Turn right	70.43%**	[0.61, 0.79]
Lobo	Left food item	73.17%**	[0.62, 0.82]
	Turn right	74.39%**	[0.64, 0.83]
Lome	Right food item	66.29%*	[0.55, 0.76]
	Turn left	69.66%**	[0.59, 0.79]

Note. Clopper-Pearson 95% Confidence Intervals and significance were calculated from two-tailed exact binomial tests. Food item choice and turn direction were initially tested as the percentage of trials where the subject chose the right food item or turned right; if the result indicated that this occurred significantly less often than chance, the tests were re-run as the percentage of trials where the subject chose the left food item or turned left, for easier comprehension. *$p < .05$. **$p < .001$.

Efficient turning by chimpanzees with food side and turn direction biases could be the result of having many trials that adhere to those biases in an efficient combination (e.g., choosing the right-hand food and turning left), with a small number of trials deviating from one of those biases, yielding an inefficient combination (e.g., choosing the left-hand food and turning left). Or it could be the result of turning efficiently even when deviating from those biases (e.g., choosing the left-hand food and turning right). We investigated this for efficiently turning chimpanzees with a food choice side bias by comparing their turning efficiency in trials where they chose the biased-side food to trials where they chose the unbiased-side food. All four efficiently turning biased chimpanzees turned significantly efficiently regardless of whether they chose the food on the side they were biased toward or the food on the side they were biased against (Table 7).

Table 7

Percentage of Efficient Trials by Food Item Choice in the FV Task

Subject	Food item choice side	% of efficient trials	95% CI
Alex	Biased toward (Right)	93.72%**	[0.90, 0.97]
	Biased against (Left)	100.00%**	[0.94, 1.00]
Dorien	Biased toward (Right)	85.29%**	[0.75, 0.93]
	Biased against (Left)	77.78%*	[0.61, 0.90]
Lobo	Biased toward (Left)	96.67%**	[0.88, 1.00]
	Biased against (Right)	86.36%**	[0.65, 0.97]
Lome	Biased toward (Right)	93.22%**	[0.84, 0.98]
	Biased against (Left)	76.67%*	[0.58, 0.90]

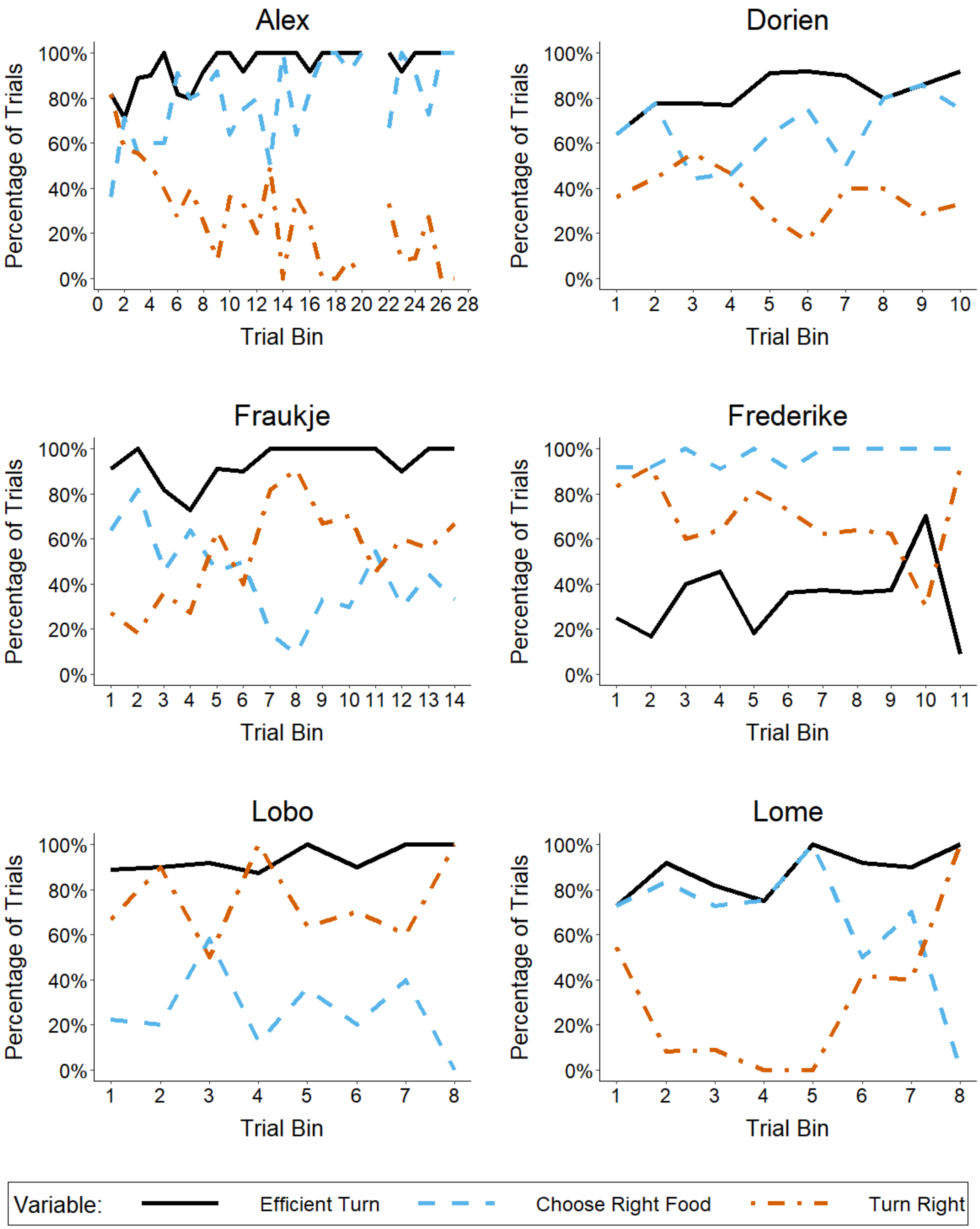
Note. Clopper-Pearson 95% Confidence Intervals and significance were calculated from two-tailed exact binomial tests. *$p < .05$. **$p < .001$.

Turning Behavior Across Trials

Figure 5 shows the chimpanzees' efficiency, food item choice, and turn direction behavior across trials. Turning efficiency significantly increased for two chimpanzees and did not change for the remaining four chimpanzees. Alex's turning efficiency increased significantly over time, and his likelihood of choosing the food item on the right increased and his likelihood of turning right (independent of his food item choice) decreased across trials (Table 8). Fraukje's turning efficiency also increased significantly over time (this effect was not significant when Phase was used in place of Trial Number in the model; see Table S2). Her likelihood of choosing the food item on the right decreased across trials. Lome's efficiency did not change significantly over time, although his likelihood of choosing the food item on the right decreased across trials. When accounting for food choice, his likelihood of turning right decreased and then increased across trials (Figure S2; as seen in Table S2, when Phase was used in place of Trial Number in the model, his likelihood of turning right increased across phases). None of Dorien's, Frederike's, or Lobo's turning behavior changed significantly over time. For all chimpanzees except Frederike, food choice and turning direction were negatively related such that the likelihood of turning right was significantly lower when the food on the right was chosen than when the food on the left was chosen, independent of trial number.

Figure 5

Efficiency, Food Item Choice, and Turn Direction across trials in the FV Task



Note. The percentage of trials in which chimpanzees turned efficiently (black solid line), chose the food item on the right first (blue dashed line), and turned right (red dot-dashed line) in the FV task, by chimpanzee. Trials are grouped in bins of 10-11 trials. The gaps in Alex's plot indicate trials for which the video was unavailable.

Table 8

Changes in Efficiency, Food Item Choice, and Turn Direction Across Trials in the FV Task

Subject	Dependent variable	Independent variable	Likelihood ratio test			*B*	Odds ratio	95% CI
			X^2	*df*	*n*			
Alex	Efficiency	Trial #	14.17**	1	279	1.18	3.26	[1.58, 6.73]
	Right food	Trial #	20.64**	1	279	0.72	2.05	[1.47, 2.86]
	Turn right	Trial #	19.00**	1	279	-1.50	0.22	[0.10, 0.49]
		Right food	191.57**	1	279	-8.20	0.0003	[0.00001, 0.006]
Dorien	Efficiency	Trial #	3.29	1	104			
	Right food	Trial #	1.42	1	104			
	Turn right	Trial #	1.74	2	104			
		Right food	42.69**	1	104	-3.01	0.05	[0.02, 0.15]
Fraukje	Efficiency	Trial #	4.06*	1	145	0.71	2.03	[0.96, 4.31]
	Right food	Trial #	6.93*	1	145	-0.44	0.64	[0.45, 0.91]
	Turn right	Trial #	5.20	2	145			
		Right food	121.46**	1	145	-5.38	0.005	[0.001, 0.02]
Frederike	Efficiency	Trial #	0.39	1	115			
	Right food	Trial #	2.99	1	115			
	Turn right	Trial #	1.26	1	115			
		Right food	0.83	1	115			
Lobo	Efficiency	Trial #	1.98	1	82			
	Right food	Trial #	1.01	1	82			
	Turn right	Trial #	0.00	1	82			
		Right food	57.19**	1	82	-4.71	0.009	[0.002, 0.05]
Lome	Efficiency	Trial #	3.13	1	89			
	Right food	Trial #	11.27**	1	89	-0.78	0.46	[0.28, 0.76]
	Turn right	Trial #	20.17**	2	89	-5.98 [a] 5.49 [b]	0.003 242.97	[0.00002, 0.33] [6.35, 9290.19]
		Right food	29.50**	1	89	-3.67	0.03	[0.004, 0.14]

Note. The interaction between Trial # and Right food was not included in any model because it was not significant. [a] Natural cubic spline one. [b] Natural cubic spline two. **p* < .05. ***p* < .001.

Summary

In the FV Task, five chimpanzees turned efficiently significantly more often than chance and one chimpanzee turned efficiently significantly less often than chance. Four efficiently turning chimpanzees had food item side and turn direction biases, but nevertheless turned significantly efficiently regardless of which food they chose first. The inefficiently turning chimpanzee also had food item side and turn direction biases. Across trials, two chimpanzees' turning efficiency significantly increased. One chimpanzee increasingly chose the food on the right and turned to the left, one chimpanzee increasingly chose the food on the left and decreasingly then increasingly turned to the right, and one chimpanzee increasingly chose the food on the right with no significant change in turn direction. Independent of trial number, all five efficiently turning chimpanzees showed a significant negative relationship between choosing the food on the right and turning right; Frederike, who turned inefficiently, did not. Table 9 summarizes each chimpanzee's turning behavior, overall and across each task.

Table 9

Chimpanzee Turning Behavior Overall and Across Trials, for Each Task

Subject	Variable	Quality Preference Task		Four Valleys Task	
		Overall	Across Trials	Overall	Across Trials
Alex	Efficiency	n.s.	n.s.	Efficient	Increased
	Food choice	n.s.	Right increased	Right	Right increased
	Turn direction	Right	n.s.	Left	Right decreased
				Turn direction negatively related to food choice	
Bangolo	Efficiency	n.s.	n.s.	--	--
	Food choice	n.s.	n.s.	--	--
	Turn direction	Right	Right increased	--	--
Dorien	Efficiency	n.s.	n.s.	Efficient	n.s.
	Food choice	n.s.	n.s.	Right	n.s.
	Turn direction	Right	n.s.	Left	n.s.
				Turn direction negatively related to food choice	
Fraukje	Efficiency	Efficient	Increased	Efficient	Increased
	Food choice	n.s.	n.s.	n.s.	Right decreased
	Turn direction	n.s.	Right decreased, then increased	n.s.	n.s.
		Turn direction negatively related to food choice		Turn direction negatively related to food choice	
Frederike	Efficiency	Inefficient	Decreased		Inefficient
	Food choice	Right	Right increased		Right
	Turn direction	Right	Became more likely to turn right after choosing the right food		Right
Lobo	Efficiency	n.s.	Decreased	Efficient	n.s.
	Food choice	Left	n.s.	Left	n.s.
	Turn direction	Left	Right decreased	Right	n.s.
				Turn direction negatively related to food choice	
Lome	Efficiency	--	--		Efficient
	Food choice	--	--		Right
	Turn direction	--	--		Left
				Turn direction negatively related to food choice	

Note. Turn direction across trials accounts for the relationship between turn direction and food choice. The relationship between turn direction and food choice accounts for trial number.

Discussion

In this study, we closely examined the turning behavior of chimpanzees in a semi-naturalistic VE to see whether they turned efficiently, and how this behavior developed over time. Only one chimpanzee turned efficiently in the first task, while nearly all chimpanzees turned efficiently in the second task. We found no consistent changes in food item side choice, turn direction, or efficiency across trials between individuals, but some evidence of consistency within individuals across tasks.

Importantly, we found that chimpanzees nearly always turned toward an out-of-view target in VE in both tasks, rather than continuing in their previous trajectory or moving in a random direction in the VE. This indicates that they knew that the target was in the VE, even though it was no longer in the FOV depicted on the screen, suggesting they had object permanence for virtual items in VE, as has been previously seen in VE (Allritz et al., 2022).

When we investigated whether chimpanzees made the shortest turn to an out-of-view target, we found limited efficient turning during early experience with VE and more efficient turning during later experience with VE. In the QP task, which was conducted after basic training in the VE, only one out of six chimpanzees turned efficiently significantly more often than chance, and one chimpanzee turned efficiently significantly less often than chance. These results are largely explained by the biases that some chimpanzees had for which side food item they chose first and/or which direction they turned. Fraukje, the chimpanzee who turned efficiently, had no biases for food item choice or turn direction and was less likely to turn right after choosing the food item on the right. Frederike, the chimpanzee who turned inefficiently, was biased toward the food item on the right and to turning right, a combination that leads to inefficient turns. The fact that only one chimpanzee turned efficiently in a task that was completed fairly early in their VE experience suggests that efficient turning may not be a behavior that arises after minimal experience with VE.

In the FV task, which was completed after the chimpanzees had additional experience navigating in VE, five out of the six chimpanzees turned efficiently significantly more often than chance and one chimpanzee turned efficiently significantly less often than chance. Fraukje again turned significantly efficiently without any food item choice or turning biases. Frederike, who again turned inefficiently, had the same choice and turning biases she had in the QP task. Three of the remaining chimpanzees turned efficiently but with biases toward the right food item and turning left, while the final chimpanzee turned efficiently with the opposite biases. It is possible that the efficient turning of these four biased chimpanzees was not due to understanding and then choosing the more efficient turn based on their first food item choice, but rather because they happened to have food item choice and turn direction biases in a combination that led to efficient turns (i.e., choosing the right food item and turning left or choosing the left food item and turning right). It is notable that out of five chimpanzees with choice and turn direction biases, four of them had biases that led to efficient turns, while only one had biases that led to inefficient turns. Importantly, when the four efficient biased chimpanzees chose the unbiased-side food item first, they also turned in the efficient direction (i.e., in the unbiased turn direction) more often than chance. This suggests that their efficiency was not due to a random combination of biases, but to actively turning in the efficient direction. Additionally, for all efficiently turning chimpanzees, we found that food item choice was a significant predictor of turn direction, over and above trial number: they were more likely to turn right when they had chosen the left food item, and vice versa. This indicates that even if their turn direction fluctuated as a function of trial number, it was also influenced by which food item they chose first, suggesting that efficient turning was not the result of a combination of biases that just happened to lead to efficient turns. Future studies could investigate this further by attempting to manipulate subjects' first choice by, for example, making one item visible for longer than the other – which has previously been shown to affect item choice in humans (Armel et al., 2008; Shimojo et al., 2003) – and then examining subjects' turn direction.

Notably, the chimpanzees' overall turning behavior is inconsistent with response learning (Hull, 1943), whereby a subject navigates via a chain of responses, in this case, touches to particular locations on the touchscreen. This would result in a subject always going to the same food item side first and always turning in the same direction. However, even in those chimpanzees with biases in both food item choice and turn direction, there were still a good portion of trials where they went against those biases; for instance, in the FV task, although Frederike went to the same food item side first in nearly all trials (96.52%), she only turned the same direction on 70.43% of trials. The within-subject variation in food side choice and turn direction indicates that the chimpanzees were not relying on a learned series of touches to the touchscreen in order to do these tasks, but were likely intentionally navigating toward the food item targets, as in place learning (Dolins et al., 2014; Tolman, 1932). This is consistent with prior research with rats showing an advantage for place learning over response learning in spatial navigation tasks in which the trials are closely spaced in time (Thompson & Thompson, 1949; Wingard et al., 2015) and the environments include a variety of stimuli (Galanter & Shaw, 1954; Tolman et al., 1946; Waddell et al., 1955), as in the tasks used here.

To investigate whether the chimpanzees' behavior changed with more experience in the VE, we examined their efficiency, food item side choice, and turn direction across trials in each task. Although at least one behavior of nearly all the chimpanzees changed across trials in the QP task, only one chimpanzee's efficiency increased, and two chimpanzees' efficiency decreased. Fraukje's increasing efficiency was probably due to her food choice and turning direction becoming more negatively related (turning right less often when choosing the right food item more often and vice versa), although the interaction between trial number and food choice did not reach significance. Frederike's decreasing efficiency was the result of her increasing likelihood of turning right after choosing the food item on the right. Lobo's decreasing efficiency was accompanied by a decrease in turning right. The remaining three chimpanzees' efficiency did not change over time.

Across the FV task, two chimpanzees' efficiency significantly increased, and none significantly decreased. Alex's increasing efficiency was likely due to a significant increase in choosing the food item on the right and a significant decrease in turning right when accounting for trial number (although the relationship between food choice and turn direction did not become significantly more negative across trials). Fraukje, whose efficiency also increased, showed the opposite behavioral pattern, as did Lome, whose efficiency did not change across trials. No other chimpanzee had significant behavioral changes over time. Despite all efficiently turning chimpanzees showing a significant negative relationship between food item choice and turn direction independent of trial number, the variation in turning behavior across trials within each task and between subjects indicates no other consistent relationship between experience in a task and turning efficiency, food item side choice, or turn direction. Some chimpanzees' turning efficiency increased across trials, while others' decreased, and changes in food item choice or turn direction did not consistently lead to stronger or weaker biases. This highlights the importance of examining the behavior of animals individually rather than in aggregate, particularly when examining behavior over time.

It is possible that the experience in each task individually was not sufficient to detect patterns in behavior. Looking at behavior across both tasks, three chimpanzees who turned neither significantly efficiently nor inefficiently in the QP task then turned significantly efficiently in the FV task, suggesting that more overall experience in VE may have led to greater turning efficiency. Additionally, fewer chimpanzees had significant changes in turning behavior across trials in the FV task (three out of six chimpanzees) than the QP task (five out of six chimpanzees), suggesting that turning behavior may stabilize over time. Finally, of the five chimpanzees who completed both tasks, two of them exhibited comparable turning behavior between the two tasks. Fraukje turned efficiently in both tasks and increased her efficiency across each task, with no overall biases. Frederike turned inefficiently in both tasks, developing biases in the QP task that continued into the FV task.

We must be cautious in drawing strong conclusions from these between-task comparisons, however. The two food items in the QP task were different and were rewarded differentially, while the two food items in the FV task were the same, which could affect the likelihood of developing food choice and turning biases in different ways in the two tasks. Preferences for different foods could have influenced which side the subject went to first in the QP task (indeed, this is what the task was originally designed to test), making them less likely to develop a food item side bias, as the location of the different foods was counterbalanced across trials. This is supported by the finding that five out of six chimpanzees had food item side biases in the FV task, but only two out of six chimpanzees had food item side biases in the QP task. However, we did find that efficiently turning chimpanzees with food item side biases in the FV task nonetheless turned efficiently when they chose the food item on the side they were biased against, indicating that their efficiency was not completely due to their biases. This is further supported by the finding that, in efficiently turning chimpanzees, food item choice and turn direction were significantly negatively related such that the likelihood of turning left was higher after choosing the food on the right than after choosing the food on the left, and vice versa (see Tables 5 and 8). Future research should examine these behaviors over a longer timescale to determine whether the patterns we observed across tasks are fully explained by task differences, and to better assess the consistency and stability of these behaviors over time.

Although our sample size was too small to analyze this directly, the individual differences in turning behavior that we observed did not appear to be related to factors such as age, sex, rearing history, or prior VE experience (Table 1). For example, Fraukje, the only chimpanzee to turn efficiently in both tasks, and Frederike, who turned significantly inefficiently in both tasks, were both female chimpanzees in their early forties at the time of testing, and with the same prior experience with VE. Alex, who had additional VE experience before the FV task, had a similar rate of efficient turning in the FV task to Fraukje and Lobo. Lome, who did not participate in the QP task, turned efficiently in the FV task more often than Frederike, who had participated in the QP task. In the future, larger and more varied samples will allow us to directly investigate how these factors are related to individual differences in turning behavior.

Some chimpanzees' turning behavior in the FV task was congruent with their performance on the intervening VE navigation task (Table S1; Allritz et al., 2022). For example, Alex and Fraukje, who had a high overall level of efficient turning and whose efficiency increased across trials, also had high path linearity and increasing path linearity across trials in the navigation task. Alex (though not Fraukje) also had relatively high success in navigating efficiently towards food in a new location. Frederike, who turned significantly inefficiently, had relatively lower path linearity to food not visible from her starting location and low success in locating food in a new location in the navigation task. However, the other chimpanzees' performances on the navigation task do not seem as congruent with their turning behavior, and more research is needed to better understand how performance in different VE tasks is related.

Turning efficiently regardless of which food item was chosen first could be the result of various strategies, ranging from lower-level associative rule learning to higher-level intentional efficiency. It could be argued that, rather than turning in the VE, the chimpanzees were merely touching the screen in the approximate location they last saw the second food item. For example, if they collected the food item on the right side first, as they approached that item, the second food item would move toward the left side of the screen until it was no longer in the subject's FOV. After collecting the first food item, the chimpanzee could touch the left side of the screen not in order to turn toward the second food item, but because that is where the second food item was last visible. However, we observed that many of the chimpanzees interacted with the touchscreen differently when they were navigating to a target on the screen and to a target off the screen. The chimpanzees tended to tap or make a vertical swiping motion to navigate to an on-screen target, but when navigating to an off-screen target, they often used a horizontal swiping motion (e.g., Videos S2-S4). These particular types of interactions are consistent with moving forward and turning in a 3D space, respectively.

Another possibility is that the chimpanzees used a single alternation rule, whereby if they went to the left food item first, they would then turn right, and vice versa. This would yield an efficient turn without any understanding of that turn being shorter than a turn in the other direction. However, a single alternation strategy does not appear to come automatically to primates, usually taking hundreds or even thousands of trials to learn (Battig et al., 1962; Livesey, 1969; Rosvold et al., 1961). And critically, in those prior studies, only one side was reinforced. In our tasks, subjects were rewarded regardless of which direction they turned; the only difference in reward between an efficient and an inefficient turn was the time taken to obtain the second reward. If this difference was sufficient to motivate the chimpanzees to learn a single alternation rule, then it would indicate that they were intentionally turning efficiently.

Lastly, efficient turning could be the result of following a rule of turning in the direction where the fruit was last seen (i.e., turning left if the second food item disappeared off the left side of the screen). If the subject took a straight path to the first food item, with little or no turning once the second food item moved out of their FOV, then the side of the screen that the second food item disappeared from and the efficient turning direction were the same. Thus, turning toward the side of the screen where the second fruit was last seen would also lead to efficient turning without requiring understanding of the turns being efficient. This possibility could be investigated by adding an automatic 90° turn in the inefficient direction after collecting the first food item, similar to what has been done in prior studies on homing and path integration (Etienne et al., 1988; Mittelstaedt & Mittelstaedt, 1982). This would change the direction of the efficient turn and unconfound the side of the screen where the second food was last seen and the direction of the efficient turn. For example, if the subject collects the food on the right, then is spun 90° to the right, the efficient turn to the second food item is now to the right, not to the left. If the subject turns efficiently, that would indicate that they were taking the shortest route to the second food item, rather than just turning in the direction that they last saw that item.

Turning behavior is just one aspect of how primates navigate VE, and it may be related to other navigation behaviors. Future research should examine how different aspects of navigation such as turning, surveying, path linearity, and angular deviation relate to each other to gain a more holistic picture of an individual's navigation behavior and ability. Future studies could also examine turning efficiency for non-food items such as moving prey or conspecifics. Additionally, as more tasks are presented in VE, it is increasingly important to compare behaviors in VE with those in the real world in order to determine whether the insights gained from VE tasks apply more generally. For example, it is currently unknown whether wild chimpanzees turn efficiently, nor whether efficient turning is important in foraging or navigation. Only one VE study so far has allowed for some comparison with wild chimpanzee navigation, due to subjects' ability to move freely in the environment (rather than being constrained by a virtual maze or building). Allritz and colleagues (2022) found that chimpanzees learned to navigate to landmarks to find food in VE, as do chimpanzees in the wild, and some chimpanzees had similar path linearity in VE to that observed in wild chimpanzees (Jang et al., 2019; Janmaat et al., 2013a; Normand & Boesch, 2009). Future studies should aim to more directly compare navigation behavior in VE and the wild, for example, by modelling VE on the actual forests and savannas inhabited by wild chimpanzees and by incorporating ecological components that have been found to influence navigation behavior, such as fruiting synchrony (Janmaat et al., 2013b), ephemerality (Janmaat et al., 2014), and terrain (Green et al., 2020).

In conclusion, one out of six chimpanzees turned significantly efficiently in an early VE task and five out of six chimpanzees turned significantly efficiently in a VE task that they completed later in their VE experience. Although for most chimpanzees, this efficient turning was accompanied by biases in food item side and turn direction, they nevertheless also turned efficiently even when they chose the unbiased food item side. The direction and change in biases across trials varied among chimpanzees, indicating no consistent between-subject progression of turning behavior in VE across trials. The number of chimpanzees with significant changes in turning behavior decreased across tasks, suggesting a stabilization in turning behavior with increased VE experience, but additional research is needed. By closely studying primate navigation behavior in VE, we can better understand how they perceive these environments and how their behavior compares to that in the real world, informing the design of future VE-based studies.

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Data Availability: Data, analysis script, and APExplorer 3D app to run the Four Valleys task are available at: https://osf.io/vbkqt/

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References

Allritz, M., Call, J., & Borkenau, P. (2016). How chimpanzees (*Pan troglodytes*) perform in a modified emotional Stroop task. *Animal Cognition*, *19*(3), 435-449. https://doi.org/10.1007/s10071-015-0944-3

Allritz, M., Call, J., Schweller, K., McEwen, E. S., de Guinea, M., Janmaat, K. R. L., Menzel, C. R., & Dolins, F. L. (2022). Chimpanzees (*Pan troglodytes*) navigate to find hidden fruit in a virtual environment. *Science Advances*, *8*(25), 1–17. https://doi.org/10.1126/sciadv.abm4754

Allritz, M., McEwen, E. S., & Call, J. (2021). Chimpanzees (*Pan troglodytes*) show subtle signs of uncertainty when choices are more difficult. *Cognition*, *214*, 1-11. https://doi.org/10.1016/j.cognition.2021.104766

Armel, K. C., Beaumel, A., & Rangel, A. (2008). Biasing simple choices by manipulating relative visual attention. *Judgment and Decision Making*, *3*(5), 396-403. https://doi.org/10.1017/s1930297500000413

Asensio, N., Brockelman, W. Y., Malaivijitnond, S., & Reichard, U. H. (2011). Gibbon travel paths are goal oriented. *Animal Cognition*, *14*(3), 395–405. https://doi.org/10.1007/s10071-010-0374-1

Ban, S. D., Boesch, C., N'Guessan, A., N'Goran, E. K., Tako, A., & Janmaat, K. R. L. (2016). Taï chimpanzees change their travel direction for rare feeding trees providing fatty fruits. *Animal Behaviour*, *118*, 135–147. https://doi.org/10.1016/j.anbehav.2016.05.014

Barth, J., & Call, J. (2006). Tracking the displacement of objects: A series of tasks with great apes (*Pan troglodytes, Pan paniscus, Gorilla gorilla,* and *Pongo pygmaeus*) and young children (Homo sapiens). *Journal of Experimental Psychology: Animal Behavior Processes*, *32*(3), 239–252. https://doi.org/10.1037/0097-7403.32.3.239

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Battig, K., Rosvold, H. E., & Mishkin, M. (1962). Comparison of the effects of frontal and caudate lesions on discrimination learning in monkeys. *Journal of Comparative and Physiological Psychology*, *55*(4), 458–463. https://doi.org/10.1037/h0047328

Beran, M. J., Parrish, A. E., Futch, S. E., Evans, T. A., & Perdue, B. M. (2015). Looking ahead? Computerized maze task performance by chimpanzees (Pan troglodytes), rhesus monkeys (*Macaca mulatta*), capuchin monkeys (*Cebus apella*), and human children (*Homo sapiens*). *Journal of Comparative Psychology*, *129*(2), 160-173. https://doi.org/10.1037/a0038936

Bicca-Marques, J. C., & Garber, P. A. (2004). Use of spatial, visual, and olfactory information during foraging in wild nocturnal and diurnal anthropoids: A field experiment comparing Aotus, Callicebus, and Saguinus. *American Journal of Primatology*, *62*(3), 171–187. https://doi.org/10.1002/ajp.20014

Byrne, R. W., Noser, R., Bates, L. A., & Jupp, P. E. (2009). How did they get here from there? Detecting changes of direction in terrestrial ranging. *Animal Behaviour*, *77*(3), 619–631. https://doi.org/10.1016/j.anbehav.2008.11.014

Coutrot, A., Schmidt, S., Coutrot, L., Pittman, J., Hong, L., Wiener, J. M., Hölscher, C., Dalton, R. C., Hornberger, M., & Spiers, H. J. (2019). Virtual navigation tested on a mobile app is predictive of real-world wayfinding navigation performance. *PLOS ONE*, *14*(3), e0213272. https://doi.org/10.1371/JOURNAL.PONE.0213272

Cushman, L. A., & Duffy, C. J. (2008). Virtual reality identifies navigational defects in Alzheimer disease and cognitive aging. *Nature Clinical Practice Neurology*, *4*(12), 638–639. https://doi.org/10.1038/ncpneuro0929

Dolins, F. L., Klimowicz, C., Kelley, J., & Menzel, C. R. (2014). Using virtual reality to investigate comparative spatial cognitive abilities in chimpanzees and humans. *American Journal of Primatology*, *76*(5), 496-513. https://doi.org/10.1002/ajp.22252

Dolins, F. L., Schweller, K., & Milne, S. (2017). Technology advancing the study of animal cognition: Using virtual reality to present virtually simulated environments to investigate nonhuman primate spatial cognition. *Current Zoology*, *63*(1), 97–108. https://doi.org/10.1093/cz/zow121

Dong, W., Liao, H., Liu, B., Zhan, Z., Liu, H., Meng, L., & Liu, Y. (2020). Comparing pedestrians' gaze behavior in desktop and in real environments. *Cartography and Geographic Information Science*, *47*(5), 432–451. https://doi.org/10.1080/15230406.2020.1762513

Etienne, A., Maurer, R., & Saucy, F. (1988). Limitations in the assessment of path dependent information. *Behaviour*, *106*(1–2), 81–110. https://doi.org/10.1163/156853988X00106

FC, M., Davis, T. L., & ggplot2 authors. (2022). *ggpattern: "ggplot2" Pattern Geoms*. https://cran.r-project.org/package=ggpattern

Firth, D. (1993). Bias reduction of maximum likelihood estimates. *Biometrika*, *80*(1), 27-38. https://doi.org/10.1093/biomet/80.1.27

Fragaszy, D., Johnson-Pynn, J., Hirsh, E., & Brakke, K. (2003). Strategic navigation of two-dimensional alley mazes: Comparing capuchin monkeys and chimpanzees. *Animal Cognition*, *6*(3), 149–160. https://doi.org/10.1007/s10071-002-0137-8

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Galanter, E., & Shaw, W. A. (1954). "Cue" vs. "reactive inhibition" in place and response learning. *Journal of Comparative and Physiological Psychology*, *47*(5), 395-398. https://doi.org/10.1037/h0059065

Gamer, M., Lemon, J., Fellows, I., & Singh, P. (2019). *irr: Various coefficients of interrater reliability and agreement*. https://cran.r-project.org/package=irr

Garber, P. A. (2000). Evidence for the use of spatial, temporal and social information by some primate foragers. In S. Boinski and P. A. Garber (eds.), *On the move how and why animals travel in groups* (pp. 261-298). The University of Chicago Press.

Garber, P. A., & Dolins, F. L. (1996). Testing learning paradigms in the field: evidence for use of spatial and perceptual information and rule-based foraging in wild moustached tamarins. In M. A. Norconk, A. L. Rosenberger, & P. A. Garber (Eds.), *Adaptive Radiation of Neotropical Primates* (pp. 201–216). Springer New York.

Garber, P. A., & Dolins, F. L. (2010). Examining spatial cognitive strategies in small-scale and large-scale space in tamarin monkeys. In *Spatial Cognition, Spatial Perception: Mapping the Self and Space* (pp. 180–196). Cambridge University Press.

Garber, P. A., & Paciulli, L. M. (1997). Experimental field study of spatial memory and learning in wild capuchin monkeys (*Cebus capucinus*). *Folia Primatologica*, *68*(3–5), 236-253. https://doi.org/10.1159/000157250

Gibeault, S., & MacDonald, S. E. (2000). Spatial memory and foraging competition in captive western lowland gorillas (Gorilla gorilla gorilla). *Primates*, *41*(2), 147–160. https://doi.org/10.1007/BF02557796

Green, S. J., Boruff, B. J., Bonnell, T. R., & Grueter, C. C. (2020). Chimpanzees use least-cost routes to out-of-sight goals. *Current Biology*, *30*(22), 4528-4533.e5. https://doi.org/10.1016/j.cub.2020.08.076

Heinze, G., Ploner, M., & Jiricka, L. (2022). *logistf: Firth's Bias-Reduced Logistic Regression*. https://cran.r-project.org/package=logistf

Hort, J., Laczó, J., Vyhnálek, M., Bojar, M., Bureš, J., & Vlček, K. (2007). Spatial navigation deficit in amnestic mild cognitive impairment. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(10), 4042-4047. https://doi.org/10.1073/pnas.0611314104

Hull, C. L. (1943). *Principles of Behavior*. Appleton-Century-Crofts.

Jang, H., Boesch, C., Mundry, R., Ban, S. D., & Janmaat, K. R. L. (2019). Travel linearity and speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. *Scientific Reports*, *9*(1), 1–13. https://doi.org/10.1038/s41598-019-47247-9

Janmaat, K. R. L., Ban, S. D., & Boesch, C. (2013a). Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. *Animal Behaviour*, *86*(6), 1183–1205. https://doi.org/10.1016/j.anbehav.2013.09.021

Janmaat, K. R. L., Ban, S. D., & Boesch, C. (2013b). Taï chimpanzees use botanical skills to discover fruit: What we can learn from their mistakes. *Animal Cognition*, *16*(6), 851–860. https://doi.org/10.1007/s10071-013-0617-z

Janmaat, K. R. L., de Guinea, M., Collet, J., Byrne, R. W., Robira, B., van Loon, E., Jang, H., Biro, D., Ramos-Fernández, G., Ross, C., Presotto, A., Allritz, M., Alavi, S., & Van Belle, S. (2021). Using natural travel paths to infer and compare primate cognition in the wild. *IScience*, *24*(4), 1-17. https://doi.org/10.1016/j.isci.2021.102343

Janmaat, K. R. L., Polansky, L., Ban, S. D., & Boesch, C. (2014). Wild chimpanzees plan their breakfast time, type, and location. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(46), 16343–16348. https://doi.org/10.1073/pnas.1407524111

Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *Animal Behaviour*, *55*(5), 1229–1243. https://doi.org/10.1006/anbe.1997.0688

Janson, C. H. (2007). Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition*, *10*(3), 341–356. https://doi.org/10.1007/s10071-007-0079-2

Joly, M., & Zimmermann, E. (2011). Do solitary foraging nocturnal mammals plan their routes? *Biology Letters*, *7*(4), 638–640. https://doi.org/10.1098/rsbl.2011.0258

Kosmidis, I., & Firth, D. (2021). Jeffreys-prior penalty, finiteness and shrinkage in binomial-response generalized linear models. *Biometrika*, *108*(1), 71-82. https://doi.org/10.1093/biomet/asaa052

Livesey, P. J. (1969). Double- and single-alternation learning by rhesus monkeys. *Journal of Comparative and Physiological Psychology*, *67*(4), 526–530. https://doi.org/10.1037/h0027310

MacDonald, S. E. (1994). Gorillas' (*Gorilla gorilla gorilla*) spatial memory in a foraging task. *Journal of Comparative Psychology*, *108*(2), 107–113. https://doi.org/10.1037/0735-7036.108.2.107

MacDonald, S. E., & Agnes, M. M. (1999). Orangutan spatial memory and behavior in a foraging task. *Journal of Comparative Psychology*, *113*(2), 213–217. https://doi.org/10.1037/0735-7036.113.2.213

McEwen, E. S., Allritz, M., Call, J., Koopman, S. E., Rapport Munro, E., Bottero Cantuarias, C. J., Menzel, C. R., Dolins, F. L., Janmaat, K. R. L., & Schweller, K. (2025). Training primates to forage in virtual 3D environments. *Behavioural Processes*, *224*, 1-14. https://doi.org/10.1016/j.beproc.2024.105126

Mendes, N., & Call, J. (2014). Chimpanzees form long-term memories for food locations after limited exposure. *American Journal of Primatology*, *76*(5), 485–495. https://doi.org/10.1002/ajp.22248

Menzel, C. R. (1991). Cognitive aspects of foraging in Japanese monkeys. *Animal Behaviour*, *41*(3), 397-402. https://doi.org/10.1016/S0003-3472(05)80840-1

Menzel, E. W. (1973). Chimpanzee spatial memory organization. *Science*, *182*(4115), 943–945.

Mittelstaedt, H., & Mittelstaedt, M. L. (1982). Homing by path integration. In *Avian Navigation: International Symposium on Avian Navigation (ISAN) held at Tirena (Pisa), September 11-14, 1981* (pp. 290–297). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-68616-0_29

Mushiake, H., Saito, N., Sakamoto, K., Sato, Y., & Tanji, J. (2001). Visually based path-planning by Japanese monkeys. *Cognitive Brain Research*, *11*(1), 165–169. https://doi.org/10.1016/S0926-6410(00)00067-7

Normand, E., & Boesch, C. (2009). Sophisticated Euclidean maps in forest chimpanzees. *Animal Behaviour*, *77*(5), 1195–1201. https://doi.org/10.1016/j.anbehav.2009.01.025

Noser, R., & Byrne, R. W. (2014). Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. *American Journal of Primatology*, *76*(5), 399-409. https://doi.org/10.1002/ajp.22181

Ohshiba, N. (1997). Memorization of serial items by Japanese monkeys, a chimpanzee, and humans. *Japanese Psychological Research*, *39*(3), 236-252. https://doi.org/10.1111/1468-5884.00057

Pedersen, T. L. (2023). *patchwork: The Composer of Plots*. https://cran.r-project.org/package=patchwork

Presotto, A., Verderane, M. P., Biondi, L., Mendonça-Furtado, O., Spagnoletti, N., Madden, M., & Izar, P. (2018). Intersection as key locations for bearded capuchin monkeys (*Sapajus libidinosus*) traveling within a route network. *Animal Cognition*, *21*(3), 393–405. https://doi.org/10.1007/s10071-018-1176-0

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rainey, C., & McCaskey, K. (2021). Estimating logit models with small samples. *Political Science Research and Methods*, *9*(3), 549-564. https://doi.org/10.1017/psrm.2021.9

Robinson, D., Hayes, A., & Couch, S. (2023). *broom: Convert statistical objects into tidy tibbles*. https://cran.r-project.org/package=broom

Rosvold, H. E., Szwarcbart, M. K., Mirsky, A. F., & Mishkin, M. (1961). The effect of frontal-lobe damage on delayed-response performance in chimpanzees. *Journal of Comparative and Physiological Psychology*, *54*(4), 368–374. https://doi.org/10.1037/h0043331

Ruddle, R. A., & Lessels, S. (2009). The benefits of using a walking interface to navigate virtual environments. *ACM Transactions on Computer-Human Interaction*, *16*(1), 1–18. https://doi.org/10.1145/1502800.1502805

Ruddle, R. A., Volkova, E., & BüLthoff, H. H. (2011). Walking improves your cognitive map in environments that are large-scale and large in extent. *ACM Transactions on Computer-Human Interaction*, *18*(2), 1–20. https://doi.org/10.1145/1970378.1970384

Sato, N., Sakata, H., Tanaka, Y., & Taira, M. (2004). Navigation in virtual environment by the macaque monkey. *Behavioural Brain Research*, *153*(1), 287–291. https://doi.org/10.1016/j.bbr.2003.10.026

Schoenberg, I. J. (1946). Contributions to the problem of approximation of equidistant data by analytic functions. Part A. On the problem of smoothing or graduation. A first class of analytic approximation formulae. *Quarterly of Applied Mathematics*, *4*(1), 45-99. https://doi.org/10.1090/qam/15914

Schweller, K. G., Allritz, M., Call, J., McEwen, E. S., Janmaat, K. R. L., Menzel, C. R., & Dolins, F. L. (2022). *APExplorer_3D: A virtual environment application for the study of primate cognition*. https://doi.org/https://doi.org/10.17605/OSF.IO/SX5PM

Shimojo, S., Simion, C., Shimojo, E., & Scheier, C. (2003). Gaze bias both reflects and influences preference. *Nature Neuroscience*, *6*(12), 1317-1322. https://doi.org/10.1038/nn1150

Stone, C. J., & Koo, C.-Y. (1985). Additive Splines in Statistics. *Proceedings of the American Statistical Association, 45*, 45-49.

Teichroeb, J. A. (2015). Vervet monkeys use paths consistent with context-specific spatial movement heuristics. *Ecology and Evolution*, *5*(20), 4706–4716. https://doi.org/10.1002/ece3.1755

Teichroeb, J. A., & Aguado, W. D. (2016). Foraging vervet monkeys optimize travel distance when alone but prioritize high-reward food sites when in competition. *Animal Behaviour*, *115*, 1–10. https://doi.org/10.1016/j.anbehav.2016.02.020

Thompson, M. E., & Thompson, J. P. (1949). Reactive inhibition as a factor in maze learning: II. The role of reactive inhibition in studies of place learning versus response learning. *Journal of Experimental Psychology*, *39*(6), 883-891. https://doi.org/10.1037/h0053915

Tolman, E. C. (1932). *Purposive Behavior in Animals and Men*. Appleton-Century-Crofts.

Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946). Studies in spatial learning. II. Place learning versus response learning. *Journal of Experimental Psychology*, *36*(3), 221-229. https://doi.org/10.1037/h0060262

Tomonaga, M., Matsuzawa, T., & Itakura, S. (1993). Teaching ordinals to a cardinal-trained chimpanzee. *Primate Research*, *9*(2), 67-77. https://doi.org/10.2354/psj.9.2_67

van der Ham, I. J. M., Faber, A. M. E., Venselaar, M., van Kreveld, M. J., & Löffler, M. (2015). Ecological validity of virtual environments to assess human navigation ability. *Frontiers in Psychology*, *6*(May), 1–6. https://doi.org/10.3389/fpsyg.2015.00637

Voinov, P. V., Call, J., Knoblich, G., Oshkina, M., & Allritz, M. (2020). Chimpanzee coordination and potential communication in a two-touchscreen turn-taking game. *Scientific Reports*, *10*(1), 3400. https://doi.org/10.1038/s41598-020-60307-9

Waddell, D., Gans, S., Kempner, P., & Williams, A. (1955). A comparison of place and response learning in very young rats. *Journal of Comparative and Physiological Psychology*, *48*(5), 375-377. https://doi.org/10.1037/h0040086

Waller, D., Hunt, E., & Knapp, D. (1998). The transfer of spatial knowledge in virtual environment training. *Presence: Teleoperators and Virtual Environments*, *7*(2), 129–143. https://doi.org/10.1162/105474698565631

Washburn, D. A. (1992). Analyzing the path of responding in maze-solving and other tasks. *Behavior Research Methods, Instruments, & Computers*, *24*(2), 248–252. https://doi.org/10.3758/BF03203502

Washburn, D. A., & Astur, R. S. (2003). Exploration of virtual mazes by rhesus monkeys (*Macaca mulatta*). *Animal Cognition*, *6*(3), 161–168. https://doi.org/10.1007/s10071-003-0173-z

Weisberg, S. M., Schinazi, V. R., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2014). Variations in cognitive maps: Understanding individual differences in navigation. *Journal of Experimental Psychology: Learning Memory and Cognition*, *40*(3), 669–682. https://doi.org/10.1037/a0035261

Weniger, G., Ruhleder, M., Lange, C., Wolf, S., & Irle, E. (2011). Egocentric and allocentric memory as assessed by virtual reality in individuals with amnestic mild cognitive impairment. *Neuropsychologia*, *49*(3), 518–527. https://doi.org/10.1016/j.neuropsychologia.2010.12.031

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Wilke, C. O. (2020). *cowplot: Streamlined Plot Theme and Plot Annotations for “ggplot2.”* https://cran.r-project.org/package=cowplot

Wingard, J. C., Goodman, J., Leong, K. C., & Packard, M. G. (2015). Differential effects of massed and spaced training on place and response learning: A memory systems perspective. *Behavioural Processes*, *118*, 85-89. https://doi.org/10.1016/j.beproc.2015.06.004

Supplementary Materials

Supplementary Video 1

Example Trial of the Quality Preference (QP) Task

https://doi.org/10.6084/m9.figshare.28497848.v1

Supplementary Video 2

Example Trial of the Single Phase of the Four Valleys (FV) Task

https://doi.org/10.6084/m9.figshare.28497869.v1

Note. The 360° turn at the beginning of the trial was programmed as part of the trial, not initiated by the subject. Black horizonal bars at the top and bottom of the screen during this turn correspond to when the subject cannot direct their movement in the environment; when the bars disappear, the subject can direct their movement in the environment.

Supplementary Video 3

Example Trial of the Double Phase of the Four Valleys (FV) Task

https://doi.org/10.6084/m9.figshare.28497893.v1

Note. The 360° turn at the beginning of the trial was programmed as part of the trial, not initiated by the subject. Black horizonal bars at the top and bottom of the screen during this turn correspond to when the subject cannot direct their movement in the environment; when the bars disappear, the subject can direct their movement in the environment.

Supplementary Video 4

Example Trial of the Horseshoe Phase of the Four Valleys (FV) Task

https://doi.org/10.6084/m9.figshare.28497920.v1

Table S1

Chimpanzee Performance on a Prior VE Navigation Task (Allritz et al., 2022)

	Food not visible at starting location (trial type 1C)		Food in new location (phase 4, probe trials)	
Subject	Path linearity across all successful trials	Median path linearity across all successful trials	# of trials food found	Median path linearity in successful trials, beyond disambiguation line
Alex	+ *	0.96	7/12	0.94
Dorien	– *	0.85	7/12	0.54
Fraukje	+ *	0.89	4/12	0.75
Frederike	+	0.61	2/12	0.83
Lobo	+	0.79	7/12	0.72
Lome	+ *	0.83	6/12	0.71

Note. *p < .05.

Table S2

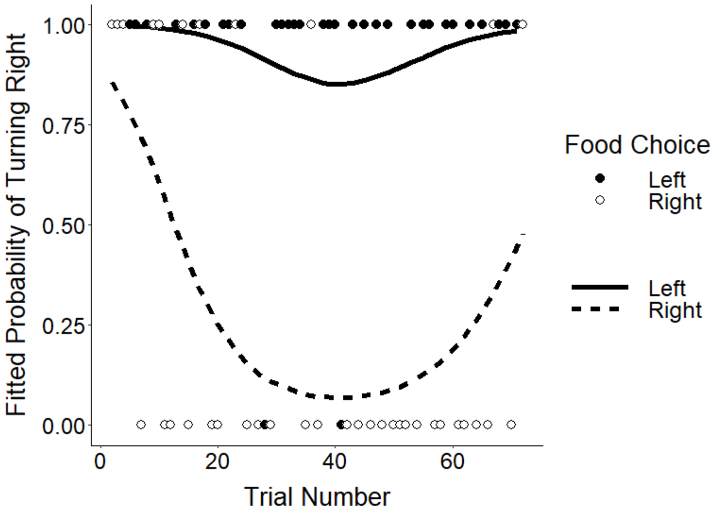
Changes in Efficiency, Food Item Choice, and Turn Direction Across Phases in the FV Task

Subject	Dependent variable	Independent variable	Likelihood ratio test			Effect	*B*	Odds ratio [95% CI]
			X^2	*df*	*n*			
Alex	Efficiency	Phase	10.76*	2	279	Linear	2.48*	
						Quad	-0.01	
	Right food	Phase	14.43**	2	279	Linear	1.70**	
						Quad	-0.11	
	Turn right	Phase	16.90**	2	279	Linear	-3.32**	
						Quad	0.12	
		Right food	191.48**	1	279		-7.55**	0.0005 [0.00003, 0.009]
Dorien	Efficiency	Phase	3.22	2	104			
	Right food	Phase	2.93	2	104			
	Turn right	Phase	1.20	2	104			
		Right food	42.18**	1	104		-2.97**	0.05 [0.02, 0.15]
Fraukje	Efficiency	Phase	2.01	2	145			
	Right food	Phase	13.84**	2	145	Linear	-1.01*	
						Quad	0.84*	
	Turn right	Phase	0.99	2	145			
		Right food	121.57**	1	145		-5.24	0.005 [0.001, 0.02]
Frederike	Efficiency	Phase	1.55	2	115			
	Right food	Phase	2.94	2	115			
	Turn right	Phase	3.01	2	115			
		Right food	1.14	1	115			
Lobo	Efficiency	Phase	3.08	2	82			
	Right food	Phase	1.22	2	82			
	Turn right	Phase	0.00	2	82			
		Right food	56.98**	1	82		-4.62**	0.01 [0.002, 0.05]
Lome	Efficiency	Phase	3.85	2	89			
	Right food	Phase	17.73**	2	89	Linear	-1.06*	
						Quad	-1.30*	
	Turn right	Phase	8.87*	2	89	Linear	0.82	
						Quad	1.70*	
		Right food	30.50**	1	89		-3.20**	0.04 [0.01, 0.15]

Note. The interaction between Trial # and Right food was not included in any model either because it was not significant or because the model containing the interaction did not converge. *p < .05. **p < .001.

Figure S1

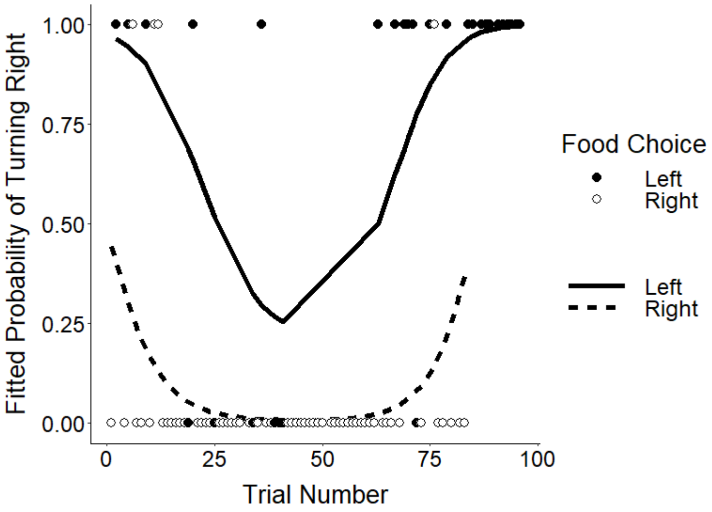
Data and Fitted Probability of Turning Right by Food Item Choice and Trial Number in the QP Task for Fraukje



Note. The lines indicate the fitted probability of turning right from a logistic regression of turn direction on trial number and food item choice. The dots are raw data, with each dot representing whether Fraukje turned right (1) or left (0) in a trial.

Figure S2

Data and Fitted Probability of Turning Right by Food Item Choice and Trial Number in the FV Task for Lome



Note. The lines indicate the fitted probability of turning right from a logistic regression of turn direction on trial number and food item choice. The dots are raw data, with each dot representing whether Lome turned right (1) or left (0) in a trial.