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Chimpanzees (*Pan troglodytes*) and Bonobos (*Pan paniscus*) Chase Prey Around Obstacles in Virtual Environments

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Apes require high volumes of energy-rich foods that tend to be patchily distributed, creating evolutionary pressures for flexible and complex cognition. Several species hunt mobile prey, placing demands on working memory and selecting for sociocognitive abilities such as predicting prey behavior. The mechanisms by which apes overcome foraging and hunting challenges are difficult to elucidate. Field investigations provide rich data sets but lack experimental control, limiting the gamut of questions they can answer, while experiments with captive subjects offer lower generalizability to real-world situations. Virtual environments

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The data are available at https://osf.io/4jqmt/.

The experimental materials are available at https://osf.io/4jqmt/.

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(VEs) present a compromise, combining experimental specificity with proxies of realistic situations. In this study, chimpanzees and bonobos moved through a three-dimensional VE using a touchscreen. All subjects learned to chase and catch moving rabbits, some exhibiting high success rates even in the presence of large obstacles. Success in trials with a first-person (FP) viewpoint was much higher than in trials presented from overhead, suggesting that the immersive nature of FP trials helped subjects to understand their location in the environment better than when they took a top-down view. Data were analyzed using generative computational agent models, identifying that subjects occasionally employed anticipatory hunting strategies, but more often used a direct chasing strategy. This study validates the use of VEs as an experimental paradigm, demonstrating that apes can understand the behavior of moving agents in situations of varying complexity and that computational modeling can be utilized to delve into behavioral data at a fine-grained level and identify which of several cognitive strategies they fit best.

Keywords: chimpanzee, bonobo, hunting, virtual environments, computational modeling

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Multiple theories have stressed the importance of foraging as a driver of cognitive evolution (e.g., Milton, 1981; Parker & Gibson, 1979; Rosati, 2017). By virtue of their large brains and associated high metabolic requirements, great apes face significant challenges when foraging for food. Their preference for patchily distributed, high-energy foods such as fruits and nuts (Knott, 2005; Tutin et al., 1991) and their associated long ranging patterns (Clutton-Brock & Harvey, 1977; Goldsmith, 1999) create a strong pressure to evolve abilities to find, remember, and revisit disparate food patches (Call, 2000; Zuberbühler & Janmaat, 2010) and to efficiently navigate between them (Janson & Byrne, 2007). Moreover, chimpanzees and bonobos show an inclination to hunt moving prey (see, e.g., Gilby et al., 2015; Hobaiter et al., 2017; Hohmann & Fruth, 2007; Wakefield et al., 2019), which implies the existence of evolutionary pressure on abilities related to recognizing and responding to the animate and reactive nature of live prey. Additionally, in some chimpanzee populations, hunting is a coordinated activity that requires the involvement of multiple individuals, which necessitates another set of cognitive abilities related to spatiotemporal coordination in fast-moving and changing situations (Call, 2000; Schradin, 2000). Even those great ape species that do not hunt live prey may have evolved related cognitive mechanisms, because they interact and coordinate activities with conspecifics, which are animate and reactive.

Understanding the cognitive mechanisms that great apes use to overcome the challenges associated with hunting is a difficult scientific task. Traditionally, research has taken one of two forms: field observations of wild or semiwild apes and experimental studies on captive subjects. Both forms of research have many benefits, as well as specific drawbacks.

Field investigations, particularly longitudinal studies that follow groups of individuals for an extended period of time, provide rich streams of behavioral data that can drive the development of hypotheses and provide the backdrop for experimental work. Field studies have the potential to deliver detailed information about animals at every level of their ethology, information that is relatively unbesmirched by human influence. However, researchers in the field cannot easily apply experimental conditions to free-ranging animals in order to ask specific causal questions, nor can they control the great variety of extraneous factors that may influence the subjects' responses to any experiments that are undertaken. These limitations in the field can make it very difficult to test hypotheses and distinguish between different explanations for observed behaviors.

Nevertheless, some studies in the wild do shed light on great ape foraging with respect to spatial memory. For example, research has shown that chimpanzees are capable of remembering the precise location of rare food trees within their territory, can reach them efficiently, and can even integrate information about previous feeding times within each tree (Normand et al., 2009), and they tend to monitor and approach trees that have previously carried large amounts of fruit (Janmaat et al., 2013). However, information regarding the cognitive strategies great apes use in hunting moving prey, and the factors influencing their decisions to hunt or forage, is rather limited. This can partly be attributed to the fact that the difficulties associated with research in the wild are particularly problematic in the context of hunting research: Great ape hunts are often extremely chaotic, involving multiple prey and predator individuals who move very quickly and at great heights in the trees, which may make it very difficult for researchers to keep track of what is transpiring (J. Mitani, personal communication, February 17, 2023).

Captive experimental work, in contrast—whether in a laboratory, zoo, or sanctuary—offers researchers the ability to control many external factors and to apply different experimental conditions to different groups of primates. This allows for very precise comparisons of responses, such that differences in behavior can be confidently attributed to a particular test. For example, one experiment showed excellent recall of food locations by a lexigram-proficient chimpanzee named Panzee. She directed human experimenters toward locations in which she had seen food being hidden, sometimes after delays of more than 3 days. She used lexigrams to inform the experimenters about the specific food item to be searched for, and she used referential pointing to indicate its precise location (Menzel, 1999). In a later experiment, Panzee and Sherman (another lexigram-trained chimpanzee) directed human experimenters toward a series of hidden foods in an order that was predicted by the foods' energy/handling profitability, meaning that they remembered what was hidden where and how much of it (Sayers & Menzel, 2012).

However, captive studies can suffer from a lack of real-world validity: The tests and conditions applied to subjects may be so far removed from anything they would experience in the wild that they offer limited power to make inferences about the animals' natural behaviors or abilities. This concern is especially acute in research on foraging and hunting: Captive experimental work on this topic generally requires either that the study is presented in a very large and extensive testing space that mimics the wild environment (which is expensive and often logistically impossible), or that it is abstracted into more simplistic tasks that suffer from lower ecological validity and so necessarily offer lower generalizability to real situations (Dolins et al., 2017). For example, the practice of directing humans toward food locations, rather than searching themselves, as was used in the aforementioned studies, is not reflective of natural behavior.

The use of virtual environments (VEs) is a relatively novel experimental paradigm that offers the possibility of a compromise between these two avenues of research. In the paradigm we report on here, subjects interact with a VE presented via a computer-controlled video screen using a touchscreen. The use of a video-game platform enables the creation and presentation of large, detailed, and endlessly configurable environments that bear a greater resemblance to field circumstances than do traditional experiments, while also maintaining the benefits of captive studies discussed above.

Primates have been tested with computer-based tasks for decades, in the service of many and varied areas of study (see, e.g., Harris & Washburn, 2005; Parrish et al., 2015; Rumbaugh, 1977). Since the 1990s, computerized tasks have been used in studies of spatial cognition in which primates are challenged to navigate an avatar or cursor around two-dimensional (2D) VEs of which they have a bird's-eye view (i.e., a view from above/a high angle). These studies have mainly focused on the collection of stationary targets (e.g., Fragaszy et al., 2009; Furuya et al., 2014; Mushiake et al., 2001), but a few have made use of moving targets (Brooks et al., 1978; Filion et al., 1996; Iversen & Matsuzawa, 2003; Jaeger, 1980; Newsom et al., 1976; Rumbaugh et al., 1989; Washburn & Rumbaugh, 1992).

More recently, researchers have also used three-dimensional (3D) VEs to test the spatial navigation abilities of macaques, bonobos, and chimpanzees (Allritz et al., 2022; Dolins et al., 2014; Sato et al., 2004; Washburn & Astur, 2003). These 3D environments have taken the form of virtual mazes of various complexities, as well as open-field, garden-style environments that simulate more naturalistic foraging situations. They display a first-person (FP) perspective (the viewpoint is rendered from the perspective of the subject's character within the VE) rather than a bird's-eye view perspective, and their elements are designed, using gradients and shadow, to create cues of depth, movement, and perspective that are absent from 2D mazes. Objects and agents in the distance may be occluded by those nearby; they appear larger as they are approached and disappear behind the field of view as the subject passes beyond them; their shading, color, and visual clarity change suitably in accordance with the direction the subject is facing in and the distance at which they are placed (Dolins et al., 2017; Washburn & Astur, 2003). A key benefit of these environments is that they allow for dynamic, player-controlled, continuous changes in the FP perspective that is displayed on the screen as the subject turns and moves through the environment. This is in stark contrast to the traditional 2D VEs, which lack shifts in perspective in response to changes in the player's position (Allritz et al., 2022). These differences between 2D and 3D VEs are very salient: The 3D experience is potentially far more immersive, allowing the subject a stronger sense of spatial displacement as they navigate via the screen. The trend in recent research toward more naturalistic, detailed 3D environments, enabled by advanced computer graphics and game engines, as opposed to simpler environments deficient in detail and dimension, opens up opportunities for research into questions that are linked more closely and explicitly to primates' behavioral ecology (Allritz et al., 2022; Dolins et al., 2017; Trapanese et al., 2019).

From the prior work on 3D navigation mentioned above, we know that chimpanzees and bonobos can efficiently navigate mazes of varying complexity, discriminating between positive and negative landmarks (Dolins et al., 2014). We also know that in an enriched nonmaze virtual setting, chimpanzees can learn to approach a landmark that signals the presence of food and flexibly deploy their knowledge of this landmark in response to changing environmental conditions (Allritz et al., 2022). Additionally, we know that in 2D formats, chimpanzees can learn to capture moving targets when they move in a predictable, consistent straight-line pattern (Iversen & Matsuzawa, 2003).

What has not yet been done is a study that investigates whether great apes can learn to navigate toward and catch unpredictably moving targets in a detailed, 3D, nonmaze virtual setting. We address this key gap in the literature. In the present study, seven chimpanzees and four bonobos were presented with a VE in which they had to navigate to collect a target—either a piece of fruit, which was static, or a rabbit, which was programmed to run away when the subject approached, and so would have to be chased. Upon collecting a target, subjects were rewarded with a piece of real fruit. Trials were run both from a 3D, FP perspective, and from a 2D, bird's-eye view perspective, to allow for a comparison between these two viewpoints. Subjects either began a trial on the same side of the virtual arena as the target, or on the opposite side. In training, there were no obstacles in the arena, so the subject could always travel in a straight line toward the target. In testing, we introduced trials with two different types of obstacle that subjects were required to circumnavigate: the forest, which could not be passed through and blocked the subject's view of the other side of the arena when the viewpoint was FP; and the lake, which also could not be passed through, but which afforded clear views across the arena in both perspective modes. The inclusion of these different obstacles enabled an investigation into whether their visual properties would have an impact on navigation in addition to their physical ones.

An additional aspect of our study that sets it apart from previous work and renders a novel contribution to the literature is the use of computational models to analyze our data, complementing the analysis methods of linear modeling that are more traditionally used in this field.

The VE methodology provides a rich data stream: The touch actions of the ape subjects and game state are recorded every 500 ms, which yields detailed behavioral responses to the dynamically changing environment. To take advantage of the behavioral record and expand the scope of our theoretical questions, we pursued a quantitative approach that involved developing a set of computational agent models that, like the subjects, are generative; they can play the VE games and generate moment-to-moment responses to the dynamic environment. Each generative model embodies a distinct theoretical hypothesis about the cognitive mechanisms that underlie the observed animal behavior and can be used to analyze and classify the full data set.

Questions and Predictions

Our work aimed to answer four key sets of questions:

1. Can chimpanzees and bonobos successfully chase and capture mobile prey in a VE? Do they improve at this over time?

   Based on their engagement and ease of training in Allritz et al. (2022) and chimpanzees' and bonobos' propensity to chase and capture mobile targets (Fruth & Hohmann, 2002;

Gilby et al., 2015; Watts & Mitani, 2002), we predicted that subjects would be able to capture mobile prey in a large proportion of trials. Additionally, based on the learning curves obtained in Allritz et al. (2022) for static prey, we predicted that subjects would significantly improve over time.

2. Can chimpanzees and bonobos successfully navigate around virtual obstacles to locate and collect targets? Do the visual properties (whether they block the view of the target) of the obstacle have an effect?

   Based on their natural ability to navigate in the real world (e.g., Boesch & Normand, 2009; Menzel et al., 2002), we predicted that bonobos and chimpanzees should be able to learn to negotiate virtual obstacles, although we expected their success rates to be relatively lower than in trials lacking an obstacle. However, we made no prediction regarding which of the two obstacles (forest or lake) should be more difficult because each comes with its own challenges. On the one hand, the forest is challenging because prey detection takes longer when the latter is located on the opposite side of the forest. On the other hand, the lake makes detection easier, but it may trigger (incorrect) direct approach responses instead of (correct) detour responses.

3. Are chimpanzees and bonobos more successful in VE when presented in a 3D, FP mode as opposed to a top-down, 2D one?

   Based on the ease with which naïve chimps mastered the FP task in Allritz et al. (2022) and the long training that is needed to master 2D mazes, which is the setup most similar to the overhead view in this task, we predicted that chimpanzees and bonobos would perform better in FP perspectives. Contrasting the FP with the top-down view amounts to pitting a less abstract but partial view of the arena against a more abstract but complete view of the arena.

4. Do chimpanzees and bonobos show any evidence of predicting where moving prey is likely to go in a VE? In other words, is pursuit focused on the target's current position, or do subjects anticipate its future position and intercept?

If the subjects anticipated as opposed to reacted to the position of the prey, we predicted that their angle of attack should deviate from the prey's current position toward its future position as determined by its current trajectory.

Should our first three predictions be borne out, this work would provide further evidence for the utility of VEs as a research tool for primate spatial cognition. It would validate VEs' use in scenarios that are of greater complexity and that require greater cognitive power and flexibility than in previous research.

Should we additionally confirm our fourth prediction, we would have clear evidence that chimpanzees and bonobos base their virtual hunting strategies on expectations of where their prey is likely to run to, rather than only using their current location. This would also open avenues for the use of VEs in social cognition research, because it would provide evidence that chimpanzee and bonobos can represent and treat moving items in VEs as goal-directed agents whose behavior can be predicted.

Predictions regarding species differences can be made by considering their respective feeding ecologies. Although bonobos and chimpanzees are highly frugivorous, bonobos supplement their diet with terrestrial vegetation such as vines, which are more homogeneously distributed than are fruit trees (Malenky & Wrangham, 1994; White & Wrangham, 1988). Additionally, resource patch sizes tend to be greater for bonobos than for chimpanzees, leading to milder feeding competition and larger foraging party sizes (White & Wrangham, 1988). Also, the abundance of chimpanzees' preferred foods tends to vary more from season to season than do bonobos' resources (Rosati & Hare, 2012). All of these factors suggest that chimpanzees face more challenging foraging problems than bonobos and therefore should possess greater spatial memory abilities. This suggestion has been borne out in experimental work on captive subjects; for example, Rosati and Hare (2012) tested 64 sanctuary-housed bonobos and chimpanzees on their ability to recover food items they had seen hidden by experimenters after a 20-min delay, finding that chimpanzees possessed more accurate spatial memory.

Every known population of wild chimpanzee exhibits hunting behavior: Their main prey species is the red colobus monkey (*Colobus* spp.), but they are also known to hunt several other monkey species, as well as rodents and large terrestrial ungulates (for an overview, see Goodall, 1986). They often hunt in groups and sometimes set out in hunting parties in which they patrol their territory together in search of red colobus (Boesch & Boesch, 1989). In contrast, it is only relatively recently that hunting by bonobos has been systematically documented; they largely prey on terrestrial ungulates like duikers that they capture opportunistically and individually, without searching for or tracking them (Hohmann & Fruth, 2007; White & Wrangham, 1988).

Although wild chimpanzees seem to exhibit a greater tendency to capture moving prey than bonobos, we cannot formulate clear predictions on how the two species' hunting abilities in VE might differ because both species capture prey and navigate around obstacles. On the whole, we do not expect the two species' performance in the current experiment to differ markedly, at least due to the aforesaid differences in their hunting strategies. There are two reasons for this. Firstly, we do not estimate their natural behavior in this respect to be so distinct as to render vastly different levels of ability in the current experimental format. Secondly, we do not expect nor aim for our VEs to provide a direct proxy to real-world behavior. We are interested in the extent to which a capacity in the one might translate to an ability in the other, but there could be a multitude of reasons why species differences in the real world may or may not map across to equivalent differences in the virtual one.

Method

Studies concerning the two species were conducted separately, with slightly different methodologies (maintaining the same overarching processes and aims), and data were analyzed separately. For this reason, they are presented here separately, titled "Chimpanzee" and "Bonobo."

Chimpanzee

Subjects and Housing

Data were collected at Edinburgh Zoo, Scotland, in two phases: May to July 2021 and January to April 2022. Seven individuals from the chimpanzee group of 16 participated regularly in the experiment (two females, five males, $M_{\text{age}} = 29.3$ years, $SD = 12.3$ years;

see Table A1 in the online supplemental materials). All subjects had experience with using the touchscreen and had undergone training to navigate 3D environments to collect stationary fruit targets (McEwen et al., 2025).

Data collection took place in the Budongo Research Unit (BRU), a specialized research area to which subjects were only allowed access during research periods (9 a.m. to 1 p.m., 7 days per week). During these times, subjects could enter and leave the BRU as they pleased. Several subjects could be in the BRU at once, but only one could participate in the experiment at a time. All participation was voluntary, and subjects could choose to stop participating at any time. They were never deprived of food or water.

Ethical approval for this project was granted by the University of St Andrews School of Psychology and Neuroscience Ethics Committee and the BRU Review Committee at Edinburgh Zoo. Edinburgh Zoo is a member of the European Association of Zoos and Aquaria, the World Association of Zoos and Aquariums, and the British and Irish Association of Zoos and Aquariums.

Materials

During research periods, a clear 23″ infrared touchscreen was installed in the testing rooms, with a computer monitor of equal size mounted behind it. Both the touchscreen and the monitor were connected to a desktop computer on which the experimental program was run. This allowed the subjects to view the experimental stimuli on the monitor and interact with them via the touchscreen. Two speakers were also connected to the computer, allowing the presentation of an audio component alongside the visual. All sessions were video-recorded.

Software

The VE application used was APExplorer_3D_CHASE, built in C# using Unity3D (Schweller, 2021). The agent in the game environment was controlled by touches on the screen. Touches anywhere on the screen other than the sky caused the agent to move toward the location that was touched. The agent would continue to move in that direction until it reached that location, collided with an impermeable object, collided with the target, or another touch was recorded. If the agent walked into an obstacle that it could not pass through, it would bounce back by a short distance.

The application recorded the location and timing of every touch that was made, as well as recording the locations of the agent and the target every 500 ms. These details were automatically encoded in a separate file for every trial. These files also denoted whether the trial was successful, unsuccessful, or aborted, as well as the subject's name, the trial and session number, and the locations of all objects in the environment.

Experimental Design

Trials. The trials took place within an octagonal arena bounded by low walls. Within the arena were the target, the subject agent, and small flowers. Outside the arena, visible over the walls, were trees and boulders to give some sense of distant landmarks. In some trials, the arena also contained a large obstacle in the form of a lake or a forest, neither of which could be traversed by the subject agent. The trials were presented in two different experimental modes: FP and overhead. In FP mode, the agent's perspective was displayed on the screen, and the agent itself was invisible. Touches to the far left- or right-hand sides of the screen caused the agent to turn in that direction, with the view on the screen shifting accordingly. As the subject agent moved closer to objects in the arena, these objects appeared larger to the subject. In this mode, the subject could see across to the other side of the arena if the trial contained a lake or no central obstacle but their view was blocked if the forest was present (Figure 1). In overhead mode, subjects saw a bird's-eye view of the arena, so everything within the arena, including the subject avatar, was visible at all times, irrespective of the type of obstacle present and which way the avatar was facing (Figure 2). In this mode, the view on the screen remained static and did not shift as the subject turned or moved their avatar.

Trials also differed by starting location: The subject either began on the same side of the arena as the target, or on the opposite side (this factor is hereafter referred to as "start relationship").

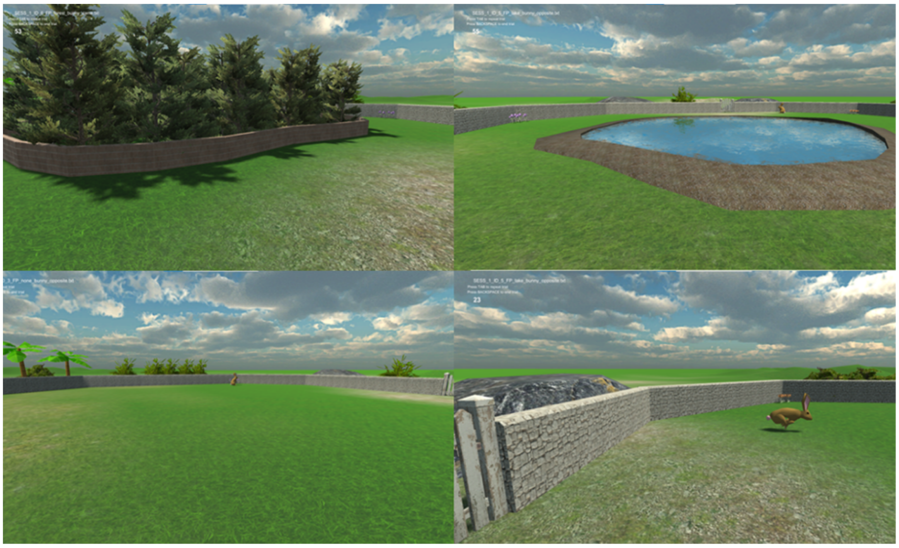
The subject avatar was an ape; the target was either a piece of fruit (an apple, a banana, or a bunch of grapes) or a rabbit. The fruit was static, while the rabbit would move away from the subject agent when approached within five meters. The rabbit's movement was determined by an A* pathfinding algorithm; its aim was to avoid the agent, and it would move away in a random direction for a short distance, and then stop. When approached again, it would move away in another random direction. It moved at half the speed of the player, meaning that it could be caught if chased. The movement of the agent was accompanied by the sound of footsteps. The rabbit made occasional squeaking noises when approached.

To succeed at a trial, subjects had to bring their agent into contact with the target, whereupon the target would rise a short distance into the air (if fruit) or fall over (if a rabbit), and a "ta-daa" sound would play. Upon collecting a virtual fruit, subjects were rewarded with their corresponding real-life fruit (e.g., a virtual apple was rewarded with a small piece of real apple). For rabbit trials, subjects were rewarded with a small piece of either apple or grape (across trials, fruit was given in the order apple–apple–grape). A trial lasted for a maximum of 60 s: If the subject failed to collect the target within this time, the trial would end and would be marked as unsuccessful.

Sessions. The experiment began with a training phase, followed by a testing phase. Each phase was split up into several sessions of 24 trials each: 12 trials in FP mode and 12 in overhead. Trials in each mode were presented consecutively, so that a session consisted of 12 trials from one viewpoint, followed by 12 trials from the other viewpoint. Sessions included 12 trials with a rabbit target, and 12 with fruit; they included 12 trials where the subject began on the same side of the arena as the target, and 12 on the opposite side. The order of presentation of these trials within a session was randomized.

Which viewpoint mode was presented first within a session was randomized during the first 4 weeks of data collection. After this point, sessions always began with FP trials, followed by overhead trials. This was because most subjects had far greater difficulty with overhead trials than with FP trials, and they could go for several trials in this mode without obtaining a reward. While the mode order was randomized, it was possible for 24 overhead trials to be presented concurrently across two sessions, which could cause subjects to lose the motivation to play. By switching to alternation of modes, subjects only had to complete 12 overhead trials before returning to the FP trials, in which they had a better chance of obtaining a reward.

Figure 1
First-Person Arena Images



Note. Top left: the subject's view at the start of a trial with a forest. Top right: the subject's view at the start of a trial with a lake, with a rabbit target visible on the other side. Bottom left: the subject's view at the start of a trial with no obstacle, with a rabbit target visible on the other side of the arena. Bottom right: an up-close view of a rabbit target, running away from the subject. See the online article for the color version of this figure.

It still occurred, however, that subjects found overhead trials so difficult that they would stop participating as soon as they got an overhead trial. It was therefore decided that if a subject left the touchscreen and refused to participate immediately upon seeing an overhead trial on 3 consecutive testing days, they would no longer be shown overhead trials. This occurred with one subject (Qafzeh), who was switched to FP-mode-only after he had completed two sessions. When the experiment was resumed in January 2022, it was decided that only Velu and Frek would continue receiving overhead trials in the training phase, and only Velu would receive overhead trials in the test. The rest of the subjects would only get trials in FP mode.

Training. At the start of the experiment, subjects got at least 12 training sessions of 24 trials each, in which there was no obstacle. In each viewpoint mode, there were six trials with a rabbit as the target, and six trials with fruit. Similarly, there were six trials in which the subject's starting location was on the same side of the arena as the target, and six where the subject started across the arena from the target. The order of these trials within each mode was randomized and counterbalanced across individuals. If subjects were successful in 10 out of 12 trials in each mode in the 11th and 12th training sessions, or 11 out of 12 trials in each mode in the 12th training session, then they could move on to test sessions. If not, they carried on with training sessions until they did reach this criterion. For some subjects, overhead mode was discontinued while they were still in training. See Table 1 for the number of sessions completed by each subject.

Testing. Test sessions were identical to training except that in each session, in each viewpoint mode, there were four trials with no obstacle, four with the lake obstacle, and four with the forest obstacle. The order of these trials was randomized and counterbalanced. There was no limit on the number of test sessions subjects received: They continued playing until the data collection period ended. See Table 1 for the number of sessions completed by each subject.

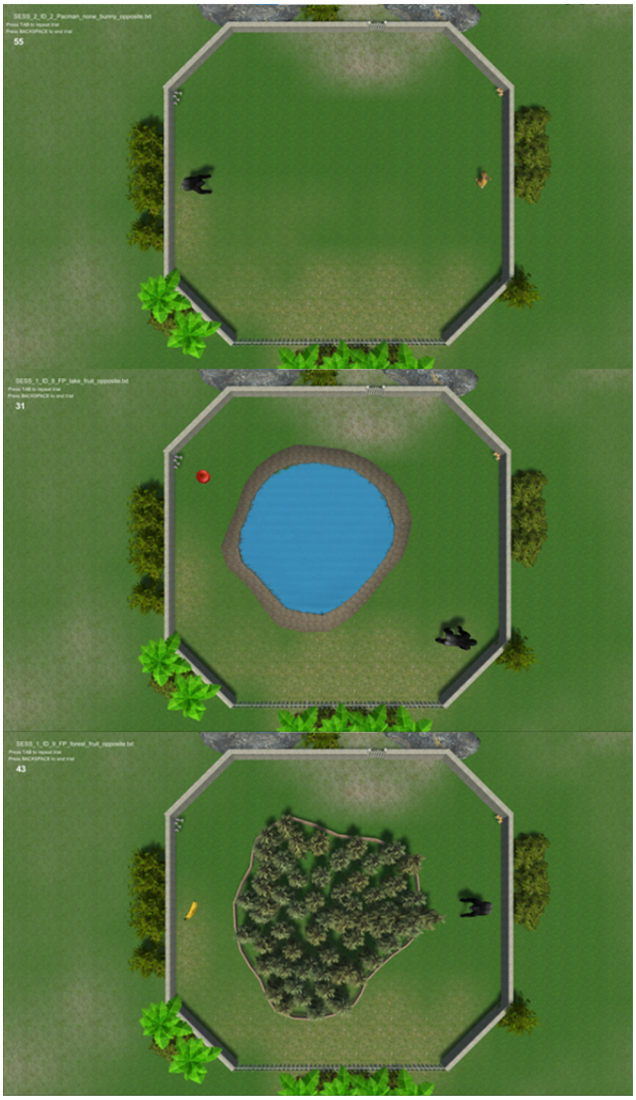
Procedure

When a subject approached the touchscreen, their name and the session and trial number they were to begin on was entered manually into the computer by the experimenter. Subjects were presented with the start screen: a blue background with a white square in the center, which they had to touch to begin a trial. When one trial was completed, the start screen was presented again, and the following trial in the sequence was undertaken. If a subject stopped participating, the experimenter noted the trial they were on, and when the subject came to participate again (whether on the same day or another testing day), they were given the next trial in the sequence. Subjects were allowed one session (24 trials) per testing day, plus (if applicable) leftover trials from an unfinished session from the previous testing day. When a subject's daily quota was reached, the experimenter switched the screen to a blank, unresponsive screen, and rewarded the subject with a banana-flavored pellet. Subjects had the opportunity to participate in this task 2–3 days per week.

If, during a trial, another ape attempted to interact with the touchscreen at the same time, the trial was aborted, and the experimenter switched to the blank screen until there was only one individual at the touchscreen. If a subject began a trial but stopped participating before the trial was completed because they were interrupted by another individual, the trial was aborted (frequency: 12.8% of total trials). Aborted trials had to be repeated.

Figure 2

Overhead Arena Images



Note. Top: subject's view at the start of a trial with no obstacle. The ape representing the subject is on the left-hand side, with the rabbit target on the right. Middle: subject's view at the start of a trial with a lake. The subject is at the bottom right, and the fruit target is top left. Bottom: subject's view at the start of a trial with a forest. The subject is on the right and the fruit target on the left. See the online article for the color version of this figure.

Table 1

Number of Sessions Completed per Chimpanzee Subject

	Training sessions		Testing sessions	
Subject	With both FP and overhead trials	With only FP trials	With both FP and overhead trials	With only FP trials
Eva	11	2	0	23
Frek	12	0	0	25.5
Kilimi	0	12	0	2
Liberius	2	10	0	2
Louis	5	35	0	1.5
Qafzeh	2	11	0	30
Velu	14	0	23	0

Note. FP = first person.

If, on the other hand, the subject stopped playing in the middle of a trial by their own choice (i.e., not due to interruption), the trial was allowed to continue running until it timed out and was not repeated later.

Bonobo

Subjects and Housing

Data were collected at the Ape Cognition and Conservation Initiative in Iowa, United States, from May to October 2021. Data were collected on four individuals from the bonobo group (two females, two males, $M_{\text{age}} = 22.5$ years, $SD = 11.7$ years; see Table A2 in the online supplemental materials). All subjects had prior experience with navigating VEs via a touchscreen (see Dolins et al., 2014, 2017).

Data collection took place in two specialized testing rooms to which the bonobos were only given access during testing periods. All participation was voluntary, and subjects could choose to stop participating at any time. They were never deprived of food or water. Ethical approval was granted by the Institutional Animal Care and Use Committee both at the Ape Initiative and at the University of Michigan. The Ape Initiative is accredited by the Association of Zoos and Aquariums.

Materials and Software

Identical to chimpanzee materials.

Experimental Design

Trials. Identical to chimpanzee trials.

Training. The first stage of training (sessions with no obstacle) was only presented to Teco and Kanzi. These sessions were identical to the training sessions given to the chimpanzees, except that as well as the FP and overhead viewpoint modes, there was also a third person (TP) viewpoint, which resembled FP except that the subject's eyeline was set slightly behind their avatar, so that they could see their avatar's body as they moved around the arena. Teco and Kanzi each received three sessions of 36 randomized trials each (three trials for each combination of start relationship [same/opposite], target [fruit/rabbit], and viewpoint [FP/overhead/TP]).

Next, Teco and Kanzi received another three 36-trial sessions of the same training, but a "Swipe" functionality was added to the game. In the previous three sessions (and in all sessions received by chimpanzees), the subjects could only move and turn by tapping on the touchscreen. Now, Teco and Kanzi could swipe along the screen to cause their avatar to move or turn.

The third phase of training was presented to all four bonobo subjects. In this phase, the TP viewpoint mode was removed, as it did not seem to be significantly different to FP. In addition, a "Drag" functionality was added, meaning that as well as tapping and swiping, subjects could drag their fingers across the screen to move themselves along. Kanzi and Teco each received two sessions of this phase, while Mali received nine, and Elikya eight. Each session consisted of 24 trials (three trials for each combination of start relationship (same/opposite), viewpoint (overhead/FP), and target (fruit/rabbit).

Testing. Testing sessions (sessions that included trials with the lake and forest obstacles) were presented to all four bonobo subjects. They were identical to those used for the chimpanzees, except for the presence of the swipe and drag functionalities. Each session consisted of 24 trials, one trial for each combination of obstacle (no obstacle/lake/forest), start relationship (same/opposite), viewpoint (overhead/FP), and target (fruit/rabbit). Trial order was randomized and counterbalanced. The aim was for each subject to complete 12 sessions. Kanzi, Mali, and Teco reached this aim, while Elikya completed only 3.5 sessions, so was excluded from the test analysis.

Procedure

Identical to chimpanzee procedure.

Transparency and Openness Statement

Data availability—data are available to readers as the additional online materials at the Open Science Framework (OSF; https://osf.io/4jqmt/; Rapport Munro et al., 2024).

Analysis code availability—analysis code is not available to readers.

Materials availability—the VE program and the files we used to run it, along with a user guide, are freely available as the additional online materials at the OSF (https://osf.io/4jqmt/).

Citation (to secondary data, materials, and/or code, including statistical packages)—all statistical packages used are cited in the text and in the References.

Reporting standards—we report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study.

Design preregistration availability—the design of this study was not preregistered.

Analysis plan preregistration availability—the analysis plan for this study was not preregistered.

Analysis and Results: Success Rates

Chimpanzee

The outcome variable of interest was the proportion of trials in which the target was acquired. We were interested in whether subjects would show the ability to collect virtual mobile prey as well as they collected stationary targets, particularly when doing so would require them to circumvent virtual obstacles. We were also interested in whether this ability would increase over time. Additionally, we were interested in whether the outcome variables would be influenced by the experimental conditions in their various combinations, and if so, to what extent.

All seven chimpanzee subjects were included in the analysis of the training data. In the analysis of the testing data, Kilimi, Liberius, and Louis were excluded, since they had completed so few sessions (Table 1). Separate analyses were performed for those subjects who completed enough overhead sessions in either training or testing for the viewpoint modes to be compared.

All quantitative analysis was carried out in R Version 4.1.2 (R Core Team, 2021). For all analyses (with the exception of the test analysis that included overhead trials) we used the R package `lme4` (Bates et al., 2015) to fit generalized linear mixed models (GLMM) (Baayen, 2008) with a binomial error function. In each analysis, the predictors of interest were included as fixed effects, and participant ID was included as a random effect. No random slopes were included in any analysis since their inclusion led to singular fits and/or lack of convergence (Beck & Bliwise, 2014). The analysis including overhead testing trials was completed using Firth logistic regression with the R package `logistf` (Heinze et al., 2022; Voinov et al., 2020).

Statistical significance of the full models was tested using likelihood ratio tests (LRTs), comparing the full models to null models that included only subject ID as predictors. Significance of individual predictors was likewise determined via LRTs using the `anova()` function to compare the full models to reduced models lacking the predictor of interest. For all statistical tests, the significance level used was $p < .05$.

Please consult the online supplemental materials for details regarding model selection for specific analyses.

Learning to Catch Mobile Prey

All seven chimpanzees learned to catch the rabbits in addition to the fruit, most requiring only the minimum of 12 sessions of training (Figure 3). Average levels of success at catching rabbits across the entirety of the training phase differed markedly between individuals (Table 2). When looking at successful trials only, in the training phase, the average latency to collecting the target was 18.6 s in fruit trials and 20.6 s in rabbit trials. In the testing phase, these latencies were 27.3 and 30.5 s, respectively.

The four subjects who completed the test phase were also able to collect moving and static targets in the presence of obstacles, all showing fairly high rates of success (Table 2). In this phase, some subjects showed improved performance in catching rabbits in comparison to the training, indicating a continuation of a learning curve; for others, success rates dipped slightly, indicating some difficulty in circumventing the central obstacles (see Table 2).

See Figure A1 in the online supplemental materials for trends in success across sessions for individual subjects.

Proportion Success in Training—FP

This analysis included data from the FP trials of all seven individuals. The predictors in this model were target type and starting position (same side of the arena as the target, or opposite), with participant ID as a random effect and session number as a control.

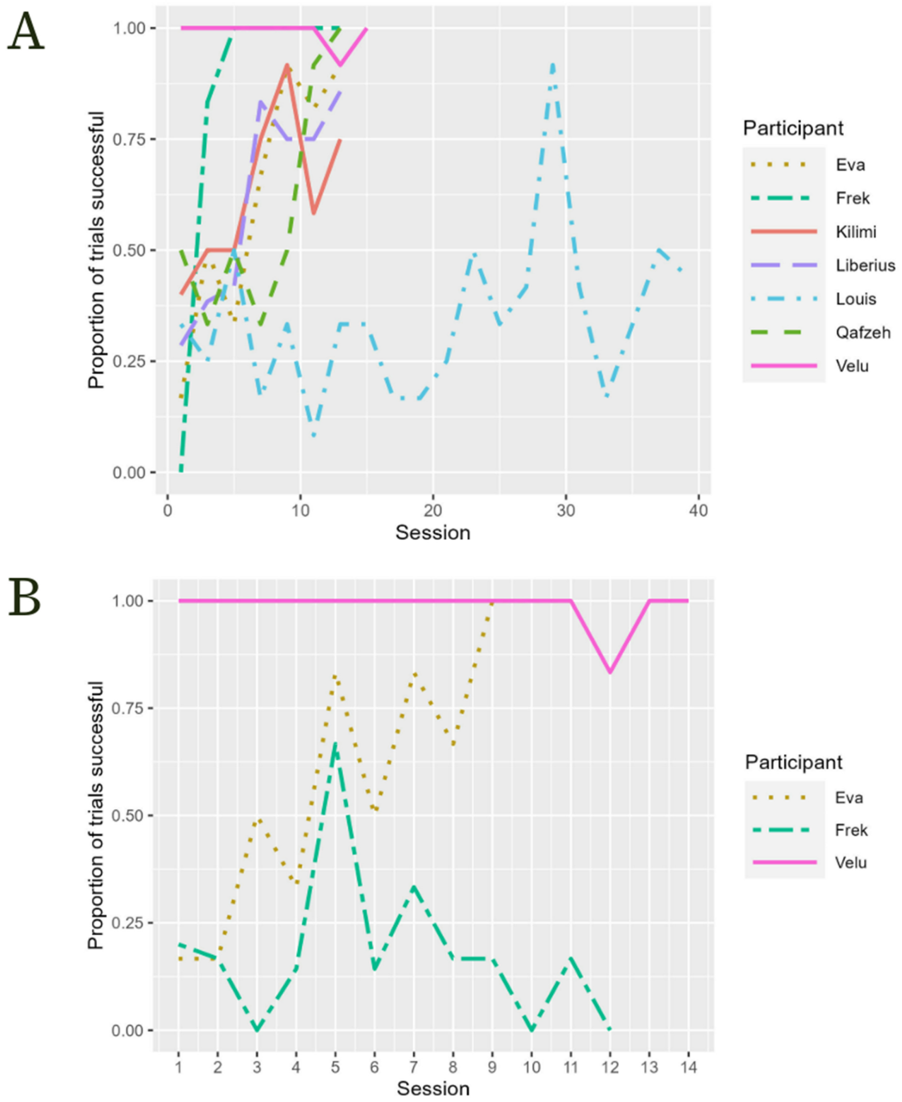
The effect of target type was significant: Subjects were significantly more likely to succeed in a trial in which the target was a piece of fruit than when it was a rabbit, $\chi^2(1, N = 7) = 44.41$, $p < .001$ (see Figure A2 in the online supplemental materials). Session number also had a significant effect: Subjects improved at catching targets over time, $\chi^2(1, N = 7) = 42.96$, $p < .001$. Start relationship was nonsignificant as a predictor of success, $\chi^2(1, N = 7) = 2.98$, $p = .08$. So, with regard to Research Question 1: Yes, chimpanzees can learn to catch moving targets in VE, although static targets are (at least initially) easier to collect.

Proportion Success in Training—FP and Overhead

An additional GLMM was fitted to compare success across viewpoint modes for Eva, Frek, and Velu, each of whom completed at

Figure 3

Proportion of Rabbit Trials Successful Across Sessions for Chimpanzee Subjects in the Training Phase



Note. (A) Success in first-person trials only. Values are plotted in two-session bins. Louis may have taken longer to reach criterion for moving to the test phase because of his poor eyesight resulting in him fixating on objects such as flowers and bushes, rather than noticing the target objects. (B) Success in overhead trials only. Only the subjects who completed over five sessions are included. See the online article for the color version of this figure.

least 11 sessions of training that included overhead trials. The fixed and random effects were the same as in the previous model, with the addition of viewpoint as a fixed effect.

The effect of viewpoint was significant, $\chi^2(1, N = 3) = 123.45$, $p < .001$: Subjects succeeded significantly more in FP than in overhead trials (see Figure A3 in the online supplemental materials). Session was also significant: Subjects improved at collecting targets over time, $\chi^2(1, N = 3) = 25.69$, $p < .001$. Target type did not have a significant effect on the likelihood of success, $\chi^2(1, N = 3) = 0.25$, $p = .617$; nor did start relationship, $\chi^2(1, N = 3) = 0.18$, $p = .672$. So, with regard to Research Question 3: Yes, a FP viewpoint does contribute to increased success rates in comparison to a top-down viewpoint. These results also reaffirm our answer to Question 1: Chimpanzees can catch moving virtual targets, and for a subset of subjects, they were no more difficult to catch than static ones.

Proportion Success in Testing—FP

This GLMM included data from the FP test sessions completed by Eva, Frek, Qafzeh, and Velu. Kilimi, Liberius, and Louis completed too few test sessions to be included. The fixed effects were obstacle (lake/forest/none), target type (fruit/rabbit), start relationship (same/

Table 2

Rabbit Trial Success for Chimpanzee Subjects

	% of rabbit trials correct in training		% of rabbit trials correct in testing	
Subject	FP	Overhead	FP	Overhead
Eva	65.3	62.7	80.6	N/A
Frek	89.0	18.3	80.1	N/A
Kilimi	65.3	N/A	N/A	N/A
Liberius	61.3	41.7	N/A	N/A
Louis	35.0	0.03	N/A	N/A
Qafzeh	59.0	0.15	69.3	N/A
Velu	99.0	98.9	80.6	77.0

Note. In training, Kilimi, Liberius, Louis, and Qafzeh each completed fewer than six sessions containing overhead trials (see Table 1), so their performance in overhead trials was not analyzed further. Note that Kilimi, Liberius, and Louis did not complete testing. FP = first person; N/A = not available.

opposite), session, and an obstacle/start relationship interaction. Participant ID was included as a random effect.

The obstacle/start relationship interaction was significant, $\chi^2(2, N = 4) = 36.84$, $p < .001$. When there was no obstacle, success rates were similarly high across the different start relationships; but when there was a lake or a forest in the arena, success only matched those of no-obstacle trials when the start relationship was same, and was much lower in opposite trials (Figure 4A). Session number was also significant, $\chi^2(1, N = 4) = 7.36$, $p = .01$: Subjects' success increased over time (Figure 4B). Target type did not have a significant effect, $\chi^2(1, N = 4) = 2.10$, $p = .15$. These results enable us to answer Research Question 2: Yes, chimpanzees showed a limited ability to navigate virtual obstacles, and no, the visual properties of the obstacle (whether or not it blocked their view of the target) did not have a large effect. Also, with respect to Question 1, we can now observe that once chimpanzees have gained sufficient experience with moving virtual targets, they can collect them as frequently as they do nonmoving targets.

Proportion Success in Testing—FP and Overhead

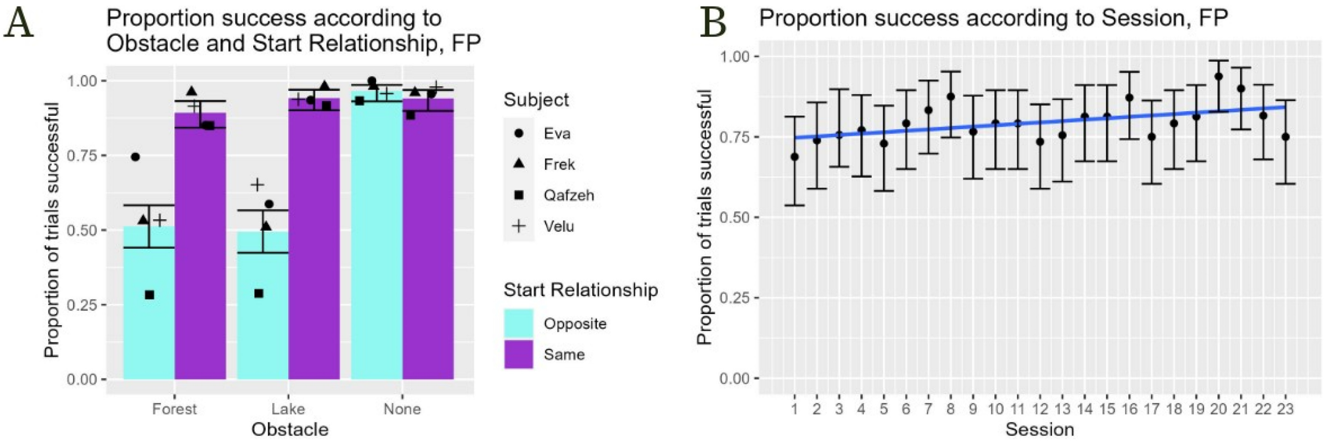
Only Velu completed sessions with both the FP and the overhead modes in testing, so an additional analysis was conducted for his data. The model that was originally fitted displayed signs of instability due to complete separation, so the analysis was conducted using Firth logistic regression, which uses penalized maximum likelihood estimation (Heinze & Schemper, 2002) and is robust to complete separation. Viewpoint, obstacle, target type, start relationship, and session were all included as fixed effects, as well as an interaction between start relationship and viewpoint. The interaction was significant, $\chi^2(1, N = 1) = 8.68$, $p = .003$: When Velu began on the opposite side of the arena from the target, trial success was higher in FP than in overhead mode; but when Velu began on the same side of the arena as the target, his success levels were similar across viewpoints, with slightly higher levels in overhead (Figure 5A). Obstacle type likewise had a significant effect, $\chi^2(2, N = 1) = 94.4$, $p < .001$: Velu's success rates reached almost 100% when there was no obstacle, but they were lower in the presence of the lake or the forest (Figure 5B). The effect of session was also significant, $\chi^2(1, N = 1) = 13.2$, $p < .001$: Velu improved at catching targets over time (Figure 5C). However, the effect of target was not significant, $\chi^2(1, N = 1) = 0.0797$, $p = .778$. These results reaffirm the answers to Research Questions 1, 2, and 3 we have already given: Chimpanzees can catch moving virtual targets; they can learn to circumvent virtual obstacles, but they still pose a significant challenge; the visual properties of the obstacle do not have an effect; and overall, they are more successful at navigating from a FP than an overhead perspective.

Bonobo

Two analyses were performed: one for the training data, and one for the testing data. TP viewpoint trials were excluded from all analyses as this condition was not presented through all training and testing stages. As with the chimpanzee analysis, GLMMs with binomial error structures were used; likewise, no random slopes were included. Again, significance of full models and individual predictors were examined using LRTs. The significance level used was again $p < .05$. Success was not

Figure 4

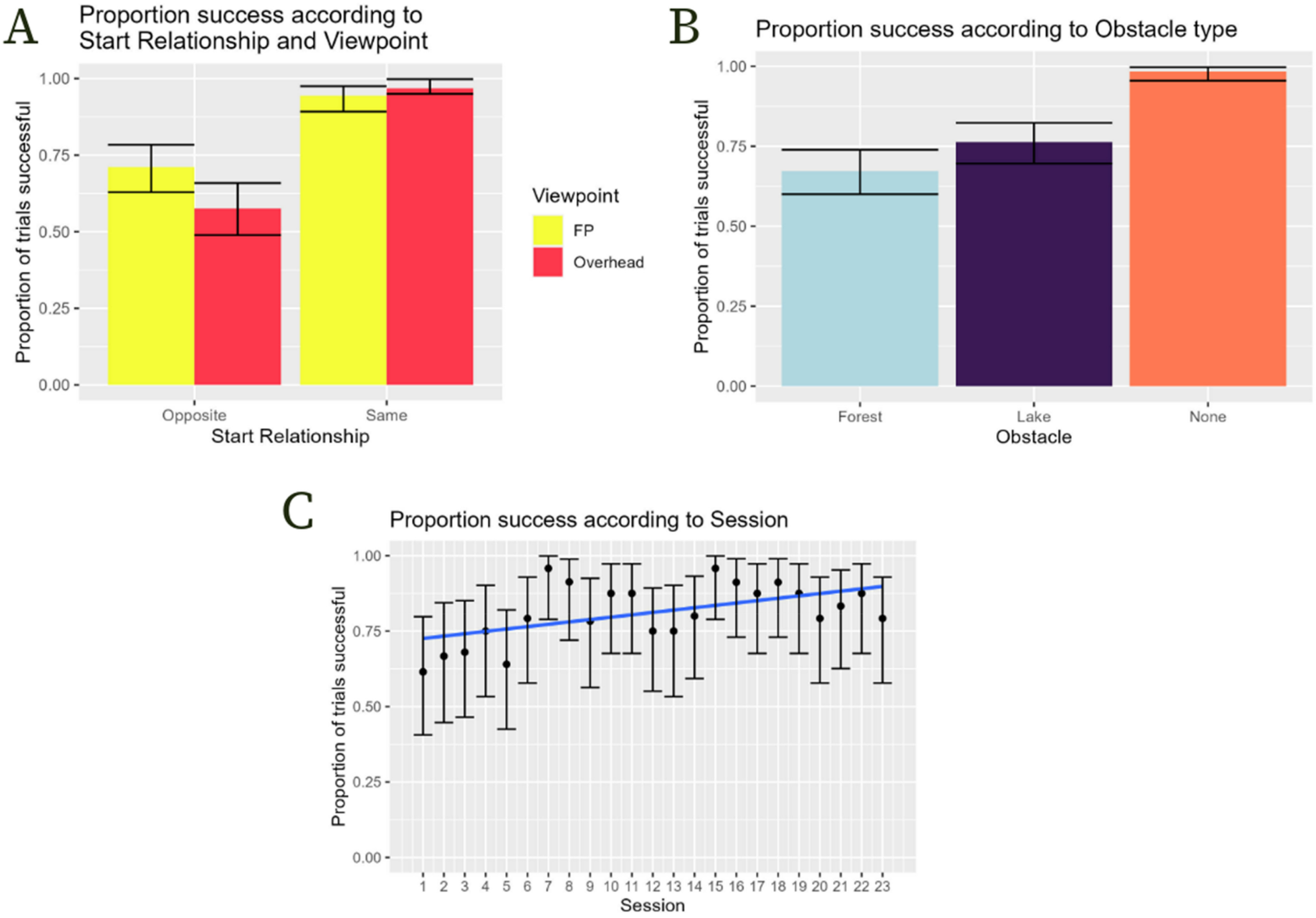
Proportion of Trials Successful in First-Person Testing



Note. (A) Symbols show success for individual subjects. (B) Only 23 sessions are included as all subjects included completed at least this many. Individual means are excluded due to lack of clarity in the graph. Error bars show 95% Clopper–Pearson confidence intervals. FP = first person. See the online article for the color version of this figure.

Figure 5

Proportion of Trials Successful for Velu in Overhead and FP Trials in the Testing Phase



Note. Error bars show 95% Clopper–Pearson confidence intervals. FP = first person. See the online article for the color version of this figure.

analyzed as a function of whether the swipe and drag functionalities were enabled, as this variable was confounded with session number.

Learning to Catch Mobile Prey

Generally, the bonobos were more successful at catching rabbit prey in training than chimpanzees were, and all can be said to have learned to catch mobile prey in the absence of obstacles, as shown by an increase in their performance over the course of the training (Table 3 and Figure 6). Elikya and Mali showed the greatest learning in their first two sessions, after which they plateau'd, while Kanzi and Teco took longer to reach maximal success. These differences could reflect the fact that the swipe and drag functionalities were enabled for Elikya and Mali from the start of their training, but only later for Kanzi and Teco. This, coupled with the success level comparison between bonobos and chimpanzees, could indicate that the addition of the ability to swipe and drag on top of touching could make it easier for subjects to traverse the VE.

When looking at successful trials only, in the training phase, the average latency to collecting the target was 19.5 s in fruit trials and 22.4 s in rabbit trials. In the testing phase, these latencies were 26.2 s and 35.0 s, respectively.

Additionally, one bonobo was reliably able to catch moving prey in the presence of obstacles: Over the course of testing, Kanzi had an average success rate in rabbit trials of 93.8%. The other two subjects had much lower success (Table 3), but still showed an upward trend in their success levels (see Figure A4 in the online supplemental materials for a graph showing individual trends).

Proportion Success in Training

The fixed effects were viewpoint, start relationship, target, and session number. Participant ID was included as a random effect.

Table 3

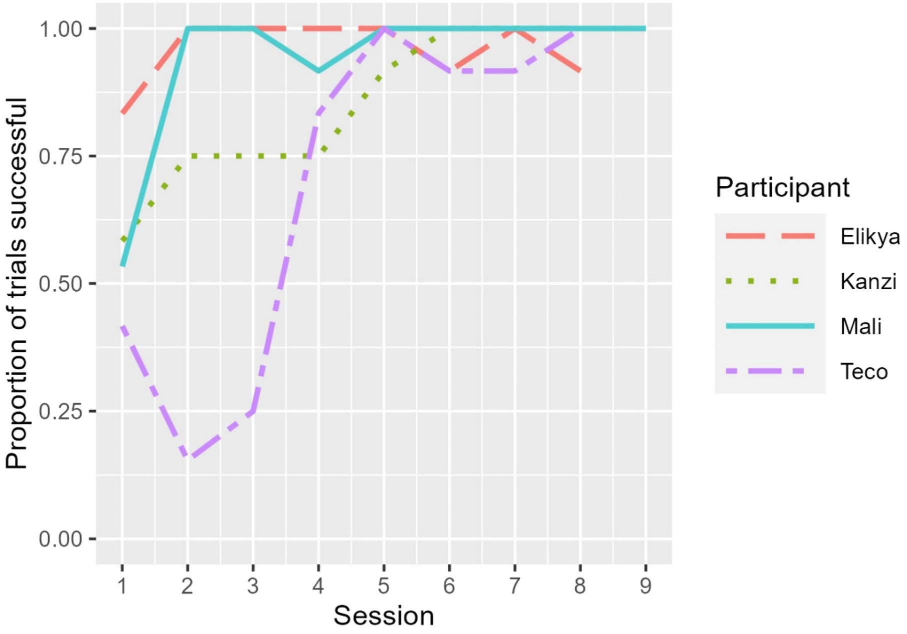
Rabbit Trial Success for Bonobo Subjects

	% of rabbit trials correct in training		% of rabbit trials correct in testing	
Subject	FP	Overhead	FP	Overhead
Elikya	93.8	97.9	50.0	30.0
Kanzi	100	68.9	91.7	95.8
Mali	92.6	93.0	54.7	36.5
Teco	75.0	61.2	65.3	50.0

Note. FP = first person.

Figure 6

Proportion of Rabbit Trials Successful Across Sessions for Bonobo Subjects in the Training Phase



Note. See the online article for the color version of this figure.

The effect of target type was significant, $\chi^2(1, N = 4) = 9.44$, $p = .002$: Subjects were significantly more successful in fruit than in rabbit trials (see Figure A5 in the online supplemental materials). Viewpoint also had a significant effect, $\chi^2(1, N = 4) = 11.27$, $p < .001$: Success levels were higher in FP than in overhead trials. Session number was also significant, $\chi^2(1, N = 4) = 100.17$, $p < .001$: Performance improved over time. Start relationship, on the other hand, did not have a significant effect on probability of success, $\chi^2(1, N = 4) = 3.35$, $p = .07$. With respect to Research Questions 1 and 3, we can therefore answer the following: Yes, bonobos can learn to catch moving virtual targets, but they succeed more frequently with stationary targets, and yes, a FP perspective contributes to greater success than an overhead perspective.

Proportion Success in Testing

The independent variables were obstacle, target, start relationship, viewpoint, session number, and an obstacle/start relationship interaction, with participant ID as a random effect.

The obstacle/start relationship interaction was significant, $\chi^2(2, N = 3) = 46.64$, $p < .001$: When there were no obstacles, subjects had high success rates across both start positions, with slightly better rates in opposite trials. But when there was an obstacle present, they had much better chances of success when they started on the same side as the target—and in both types of obstacle trial, irrespective of start relationship, success levels fell short of those seen in no-obstacle trials (Figure 7A).

Viewpoint was significant, $\chi^2(1, N = 3) = 9.82$, $p = .002$: The subjects overall were significantly more successful in FP than in overhead trials (Figure 7B). The exception was Kanzi, who despite doing far better in FP trials in the training phase, performed slightly better in the testing phase when trials were overhead. Target was also a significant predictor, $\chi^2(1, N = 3) = 37.72$, $p < .001$: Probability of success was higher in fruit than in rabbit trials (Figure 7C). Session number was also significant, $\chi^2(1, N = 3) = 26.65$, $p < .001$: The bonobos improved at catching targets over time (Figure 7D).

As with the chimpanzees, we can give the following answer to Research Questions 2 and 3: Bonobos can learn to a certain extent to navigate virtual obstacles, but they succeed far more frequently where no obstacle is present; the visual properties of the obstacle do not have a significant effect; and the use of a FP perspective contributes toward better performance. Unlike the chimpanzees, bonobos overall remained more skilled at collecting stationary targets over moving ones throughout the course of the experiment.

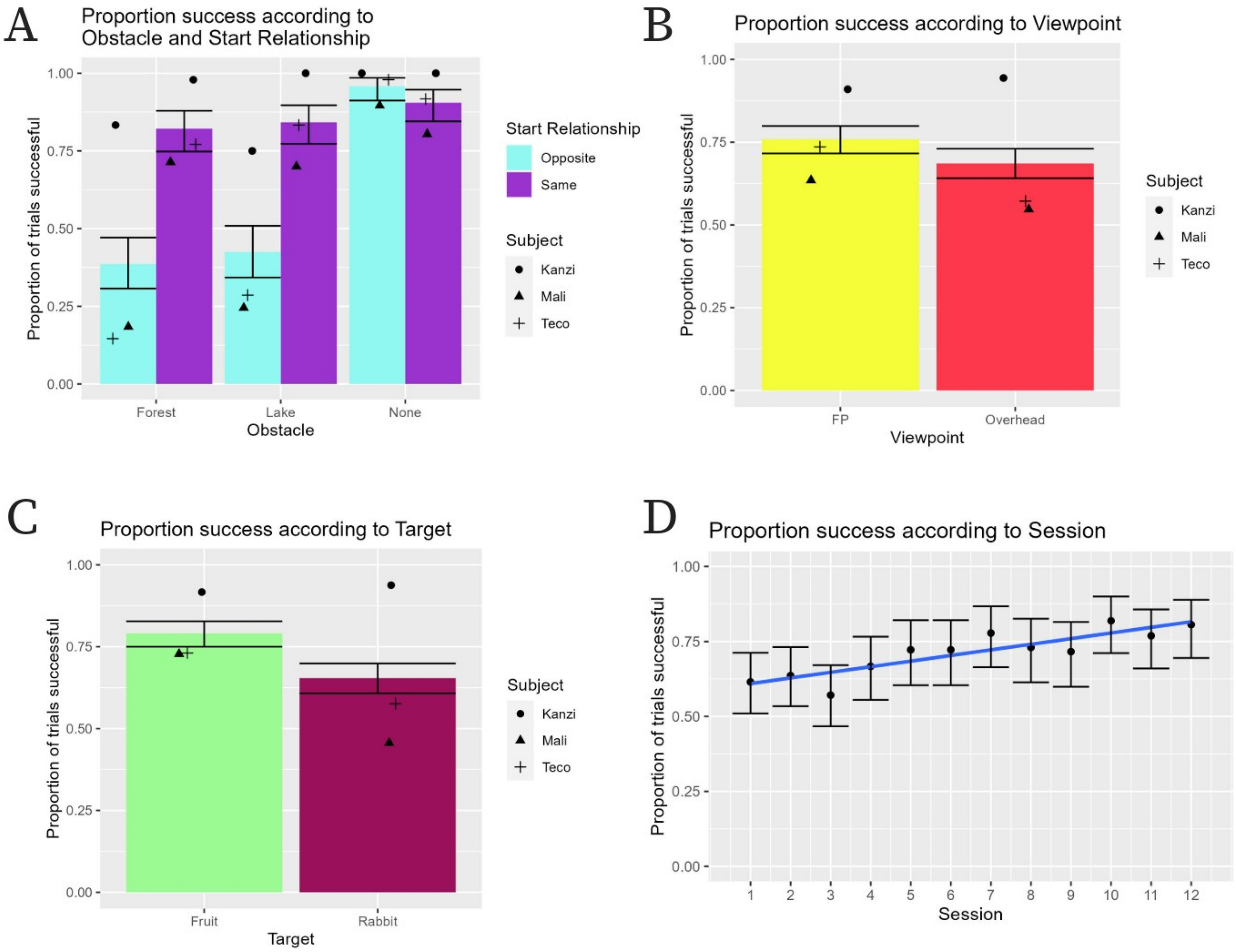
Analysis and Results: Computational Modeling

We utilized a computational modeling approach to address our final research question: Do the apes anticipate where the rabbit will move and try to intercept it, or alternatively, do they simply directly tap on the prey's current location? Although the question is easy to state, answering it from the behavioral data is challenging, because at some moments the two strategies might predict the same or very similar actions, and because the touch responses of the animals are inherently noisy.

To distinguish between these possibilities, we designed two models of hunting behavior: one that moves directly toward a target's current position, and one that computes the best angle to intercept a moving target and moves in that direction. We also included a random model that moves in each direction with equal probability. If our models of hunting behavior recapitulate the observed animal

Figure 7

Proportion of Trials Successful for Bonobo Subjects in the Testing Phase



Note. Error bars show 95% Clopper–Pearson confidence intervals. Symbols show success for individual subjects. See the online article for the color version of this figure.

behavior, then they should outperform a baseline random model. We analyzed the observed behavior by examining the similarity of each within-trial decision—twice per second—to each model, integrated across these moment-to-moment similarities using probabilistic (Bayesian) inference to handle noise and ambiguity, and used these inferences to predict which model is most likely to have generated the behavior across the trial. As we show below, an important byproduct of this analysis is that the models can be used to automatically identify moments of behavior which help to discriminate between the two cognitive strategies.

Hunting Strategy Models for Experiments 1 and 2

Sequential Decision-Making Formulation

We treated the FP VE rabbit scenarios of Experiments 1 and 2 as a Markov decision process (Sutton & Barto, 2018), a model of sequential decision making where subjects are presented with a sequence of observations and are given the opportunity to select an action at each time step, that is, a particular tap location using the touchscreen.

Our aim was to discriminate between two distinct behavioral strategies, which we refer to as direct and intercept. We formulated our computational agent models as policies (using the term from reinforcement learning), which are mappings from observations to actions (Sutton & Barto, 2018). In other words, a policy is a computational function that takes as its input an observation of the current state of the world and outputs an action selection. We will use the words “models” and “policies” interchangeably to refer to these functions. Like apes, the models can play the VE game, because they are able to make action choices for any given sequence of observational inputs. In some cases—for example, when the rabbit prey is stationary—the direct and intercept models will make the same action selections, but in other cases they will differ.

Policies are powerful representations of behavioral strategies and are adopted in nearly all modern AI approaches to autonomous agent design. In their most general form, policies need not select a single action given an input state observation but rather may output a probability distribution over a set of actions, from which a single action may be (probabilistically) sampled. Such policies are stochastic policies, with deterministic policies (always selecting the same single action for a given input) as special cases.

For our data analysis purposes, we exploit this generality and formulate our competing models as stochastic policies (Daw, 2011). The reasons for this are straightforward. There is stochastic noise in the apes' behavioral responses, so that even if they are strictly following a particular strategy their responses may deviate with some error probability, perhaps tapping a little to the left or a little to the right of the target. In our Bayesian data analysis, if we are matching such errorful responses to a deterministic policy that assigns probability 1.0 to a single action and zero for all other actions, we will soon find that any deterministic model fits actual behavior with probability zero—an unhelpful result. Thus, we must formulate direct and intercept in a way that assigns nonzero (though perhaps very small) probability to all possible actions, given simple assumptions about response error distributions that we describe below and in Figure 8.

For the observational state inputs, we could have provided our models with the same pixel-based video input as our ape subjects saw on the screen (as is done in modern AI reinforcement-learning approaches to video game play). But this imposes the added complexity of computer vision, and our interest here is not in how the apes perceive and integrate contextual information from a sequence of FP views. We therefore make a simplifying assumption and provide our models directly with the location of the target, player, and obstacles, and restrict our analyses to behavioral trajectories in which the prey is in view. Future work can relax this assumption and explore directly the apes' ability to deal with FP pixel input and prey that is out of the field of view.

In what follows, we provide details about the input states and output action space, followed by the formulation of the two models.

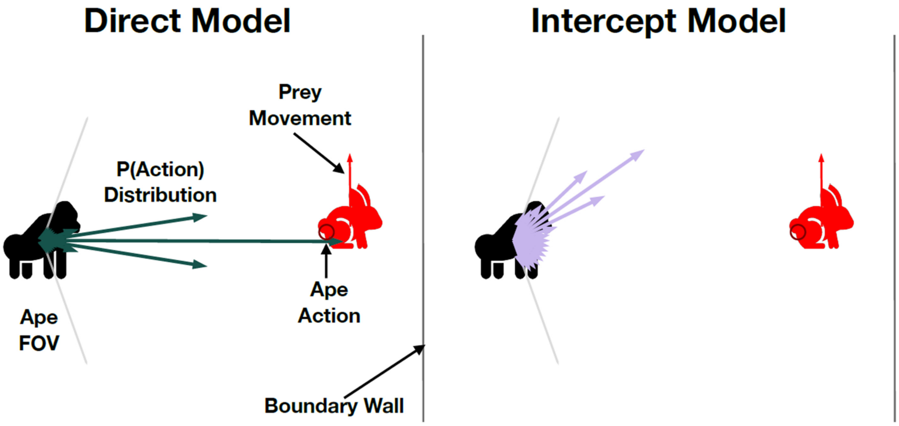
Input States. All models received the player location (in *X*, *Y* coordinates), absolute heading, target location and target heading, obstacle presence, and an indication of whether the target was currently moving. The models had full knowledge of arena and obstacle boundaries. Since the models operated with "full observability," that is, enough information to completely reproduce the current arena state, we use the term "state" to refer to the information supplied to the models.

Output Actions. Participant players tapped in a continuous action space, whereby touching on a particular point in the arena would result in the player moving toward the touched point. We simplified analyses by reducing point actions to angle actions, ranging from −70° (left) to +70° (right). We then collapsed all movement angles into 17 discrete bins (one straight-forward direction and eight binned angles to either side, each bin interval 8.75° wide). This yielded a total of 17 possible actions. A touch action was coded into these bins by computing the angle between the player's current heading and the touched point. The angle was then replaced with the bin that contained it. This maps the continuous action space into a discrete action space more conducive to computational modeling.

Direct Model. The direct model moves toward the target's current position regardless of the target's movement. This model only uses current player location, heading, and current target location. If the target is in the participant's view, the direct model computes the angle from the player's heading to the target location. The model then returns the closest available action to this angle (see

Figure 8

Top-Down View of a Single Decision Illustrates the Divergent Predictions of the Direct and Intercept Models



Note. Both panels show the same state: The prey is moving perpendicular to the ape's FOV from right to left in front of a boundary wall. Each arrow coming out of the ape represents a possible direction the ape can move toward. The length of each arrow is proportional to the probability of the action in that direction under the direct (left, green/dark gray) or intercept (right, blue/light gray) model. The highest-probability action (and hence longest arrow) for the direct model (left, green/dark gray) is the direction directly toward the prey's current position, while the highest-probability action for the intercept model (right, blue/light gray) is toward efficiently intercepting the prey where it will be by the time the ape reaches it. FOV = field of view. See the online article for the color version of this figure.

binning under Output Actions section). If the lake obstacle blocks the direct path between the player location and the target position, then direct returns no preference over actions (the uniform random distribution). Note that the forest obstacle, if between the player and the target, would occlude the target from view.

Intercept Model. Given the participant's location and heading, target's location and heading, whether the target is currently moving, and obstacle information, the intercept model selects the action that would best intercept the moving target. If the target is not currently in view, then intercept returns no preference over actions (the random distribution). We split situations with the target in view into several cases: If the target is not in motion, then intercept simply returns the direct model's preference. If the target is in motion, then intercept solves for the angle at which the player could collide with the moving target, accounting for the relative speeds of the player to the rabbit (2:1). If this angle requires crossing an obstacle, the model returns no preference over actions (the random distribution). Otherwise, the model returns the action corresponding to this angle.

Modeling Tap Error. The direct and intercept models as described above select a single action (or no-action), but for the reasons outlined earlier we must account for tapping error—the models must compute a probability distribution that assigns some nonzero probability to all actions. The online supplemental materials document describes in detail how we computed this distribution. In brief, we used an approximately Gaussian tap error that assigned high probability to the model's preferred action (as described above, e.g., direct angle to target for direct), medium probability to the nearby action angles, and very low probability to all other actions. We fitted the parameters of this distribution to individual ape players' tap errors as estimated on a subset of trials in which the rabbit is stationary and in direct unobstructed view. These trials were not used in the remaining analyses.

Figure 8 illustrates this probability distribution for the two models using an exemplar state. For the direct model (Figure 8, left), the length of the green arrows is proportional to the probability assigned to the corresponding action. There are 17 actions in total; most of the probability mass is on the center and immediate left and right arrows but there is nonzero probability on all the remaining actions. Similarly for the intercept model (Figure 8, right) the blue arrows represent the output probability distribution over actions given the exemplar state where the rabbit is moving up. In this case the highest probability actions are not directly on the target but in the direction that would best intercept the moving target.

Random Model. To account for the possibility that the subjects used a strategy that is not explained well by either the direct or intercept models, we included a random model in the analysis. The random policy assigns equal probability to every action regardless of the state. Thus, actions that are assigned very low probability by direct or intercept would be assigned higher probability by the random model, which has no preferred action.

Data Selection. For these analyses we included trials across both Training and Testing phases. Because chimpanzees and bonobos succeeded much more frequently in FP trials, we excluded overhead trials from our model-based analysis. Our experiments recorded instantaneous state information (i.e., ape and prey locations, etc.) at 500-ms intervals (henceforth "time steps"). Since subjects could execute actions multiple times during a time step, touch actions were recorded continuously. We describe how touch actions were matched to experimental states in the online supplemental materials.

To assess whether primates chase moving targets directly or compute and exploit intercepting paths, we further focused our analysis on portions of trials where subjects could feasibly employ either of these strategies. To select only moments where intercepting or direct chasing were available, we removed time steps occurring before the rabbit target had first moved. This focused the analysis on states where the participant had found the target and was close to catching it, since the rabbit did not move until the player entered within five virtual meters of the rabbit (note that before the rabbit has moved, both the direct and intercept models make the same predictions). We also removed time steps after the rabbit target had moved but had never entered the subject's FP field of view. This eliminated occasions when the subject had maneuvered near the rabbit (i.e., approaching from the side) without knowing it was there.

Analysis. Our goal is to infer which model best explains how the primates behaved when chasing the virtual moving prey. We do this first by analyzing the behavior of each primate on individual trials, asking our question at the trial level. Recall that each model policy maps a state to a probability distribution over a discrete set of actions. Thus, at each state in the trial, a model policy tells us how likely the actual observed action is given that policy. Intuitively, each observed action provides a piece of evidence for or against a model, and as we observe each action in the trial, we can successively update our belief about which model best explains the sequence of actions. At the end of the trial, our belief will be represented as a posterior probability distribution over models. Thus, our analytic problem is to convert a sequence of probabilities over actions to summary probabilities over models.

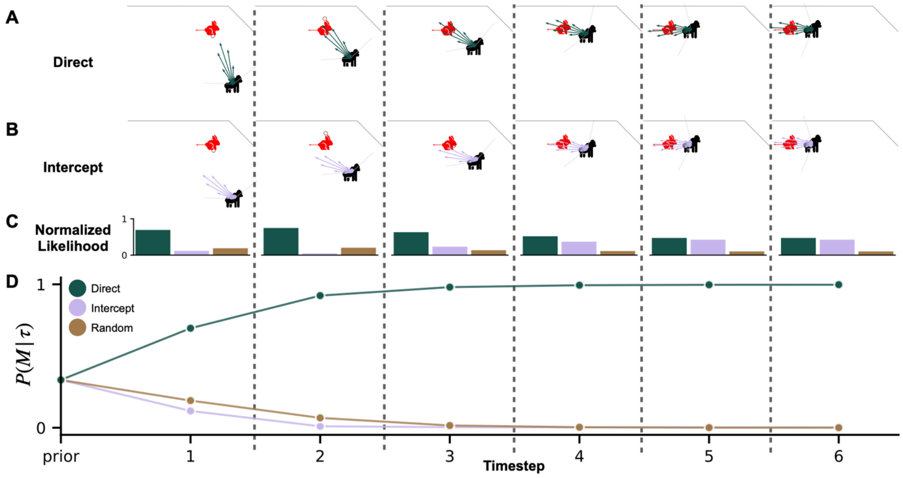
Bayesian Inference Effectively Identifies Trajectories Matching Each Strategy

Figure 9 shows this dynamic in the last six actions of one trajectory in a bonobo trial (time left to right), over approximately four and a half seconds. The top and middle rows show a sequence of top-down views at each time step (the ape player sees a FP view). Both rows are depicting the same trial where the ape is moving up and to the left and the rabbit is moving to the left; the top row shows the probability distribution over actions for the direct policy (green arrows), and the middle row the intercept policy (blue arrows, where arrow length is proportional to action probability as in Figure 8).

In each top-down view, the open circle shows the actual touch point of the ape player. For example, at Time Step 1, it is clear that the direct policy assigns relatively high probability to the actual touch point and the intercept trial assigns relatively low probability (because to intercept the player should tap to the left of the rabbit, anticipating its future position). We refer to these policy-assigned action probabilities as likelihoods, and they are depicted in the bar graphs at each time step. For example, at Time Step 5, both the intercept and direct policies are assigning approximately the same likelihood to the observed action.

Figure 9

Model-Based Analysis of a Single Bonobo Trial Best Fit by the Direct Model



Note. Six sequential actions (in this case, over ∼4.5 s) at the end of a successful trial with predictions made by the direct (A, green/dark gray) and the intercept (B, blue/light gray) models. Each frame shows the state of the ape, the prey and its trajectory, the direction chosen by the ape, and the model prediction distribution. In the first few time steps, the models make divergent predictions but make nearly the same prediction in the final time steps. (C) Normalized likelihood of the chosen action for each time step. (D) The evolution of the posterior probability $P(M \mid \tau)$ for the three models. They are initialized with a uniform prior (⅓) but rapidly diverge from the first time step because of the divergent likelihoods. See the online article for the color version of this figure.

The bottom line graph shows the evolving posterior belief over the three models as the incremental evidence is accumulated. The belief probabilities always sum to one. The belief starts at an uninformative prior probability that assigns equal belief to all three models (⅓, ⅓, ⅓, the greatest possible uncertainty). In this trial, even though the last two actions are matched equally well by the direct and intercept models, the posterior belief remains high in favor of direct (and thus against intercept) because the evidence in favor of direct is very strong in the first three time steps. At the end of the six time steps, we conclude there is strong evidence in favor of the direct policy for this trial.

Figure 10 shows a more interesting six-step trajectory from one of the chimpanzees. In this trial, the first three time steps weigh slightly in favor of intercept and the fourth time step is best matched by direct, so that at Time Step 4, both models are given roughly equal probability. But the final two taps provide strong evidence in favor of intercept over direct (the anticipatory tap is particularly clear at Time Step 5) and the cumulative evidence leads to a final posterior that is largely in favor of intercept, though with significant probability mass still on direct.

Note that the examples shown in Figures 9 and 10 serve the purpose of illustrating how the models might return differing predictions at individual time steps. They are not intended to be analyzed on their own but summed together and analyzed as a whole.

We can now identify for each trial the model policy with the highest end-of-trial posterior belief. Please see the online supplemental materials for how we utilized Bayes' rule to accumulate the policy likelihoods over an entire trial to denote a posterior belief. If the ape subjects were catching the rabbit primarily by predicting future movements and selecting a path to intercept, we would expect a greater percentage of trials to be best fit by the intercept policy. If instead subjects caught the rabbit by chasing the target's direct position without intercepting, we would expect a greater percentage of trials to be best fit by the direct policy. If subjects acted according to a strategy unlike direct or intercept, we would expect a greater percentage of trials to be best fit by the random policy.

We performed the same analyses separately for chimpanzees and bonobos with no differences in methodology. All analyses were conducted using Python (https://www.python.org).

Results

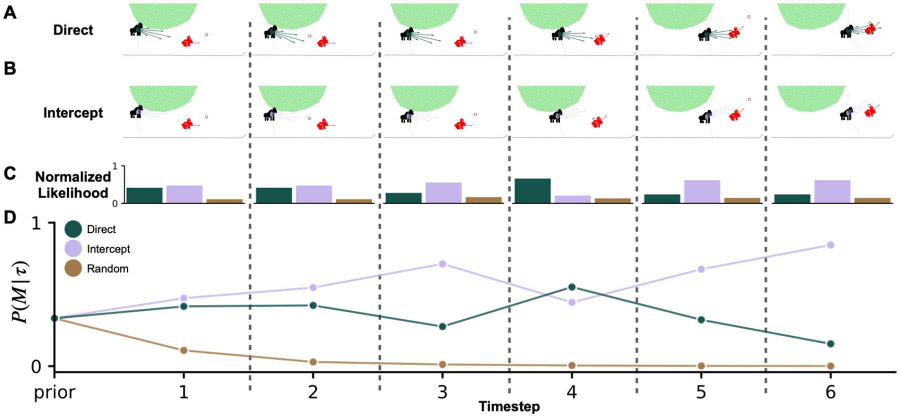
Chimpanzee

Chimpanzees Mostly Chase Targets Directly. For all subjects except Eva and Velu, no trials were best fit by the random model (Velu: 0.500%, of trials best fit by random, Eva: 0.653%) indicating little support for hunting strategies other than direct or intercept. The vast majority of trials for each participant were best fit by the direct model (Louis: 77.9%, Liberius: 84.4%, rest: above 91.6%). Only a small portion of trials for each participant were best fit by intercept (Louis: 22.1%, Liberius: 15.5%, rest: below 8.30%) (Figure 11). This suggests that overall, chimpanzees relied on chasing moving targets directly rather than predicting trajectories and heading off targets.

We inspected actions with the highest likelihoods for each model across subjects. For direct, our analysis revealed moments where an intercept path was feasible, but subjects chose to aim at the target directly. For intercept, the analysis revealed moments where chasing the target directly was viable, but subjects chose to take an intercepting route. We observed clear intercept events in the top five highest intercept likelihood actions (4/5 from Velu's trials; see Figure A6 in the online supplemental materials), in which the rabbit was in view

Figure 10

Model-Based Analysis of a Single Chimpanzee Trial Best Fit by the Intercept Model



Note. The last six actions over 3.5 s at the end of a successful trial with predictions made by the direct (A, green/dark gray) and the intercept (B, blue/light gray) models. Each frame shows the state of the ape, the prey and its trajectory, the direction chosen by the ape, and the model prediction distribution. The green semicircle represents the position of the obstacle. The models make similar predictions in the first two time steps but diverge later in the trial. (C) Normalized likelihood of the chosen action for each time step. (D) The evolution of the posterior probability $P(M \mid \tau)$ for the three models. Random is discounted after the first two time-steps but intercept does not emerge as the best fitting model until evidence is integrated across the entire trial. See the online article for the color version of this figure.

moving orthogonally to the subject and the subject chose to aim at the rabbit's future location.

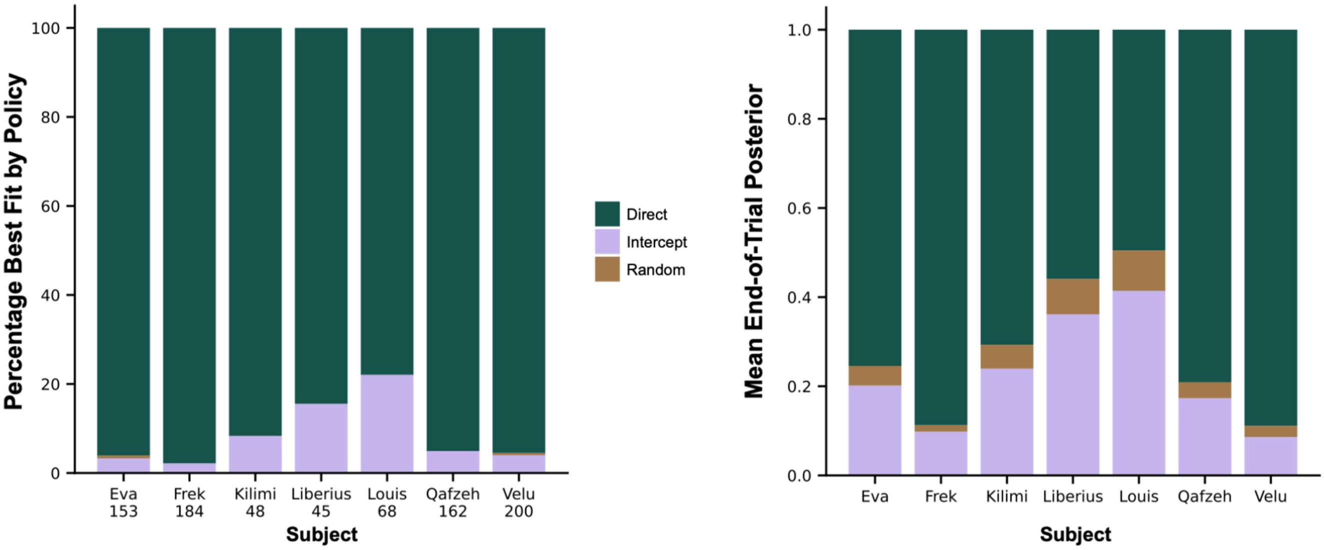
This is corroborated by inspection of the trials for which intercept was the best fitting model. In one trial, Velu hunts the rabbit, chasing directly for one state but switching to aiming ahead of the rabbit, in anticipation of its movement (see Figure 10). Our inference analysis tracks these shifts (Figure 10, Time Steps 2–3 and 4–5).

Bonobo

Bonobos Mostly Chase Targets Directly. The vast majority of trials were best fit by the direct policy (>79.6% for all four subjects, >94.1% for Mali, Kanzi, and Elikya) (Figure 12). No trials were best fit by the intercept policy for Elikya or Kanzi, while less than 4.71% of Mali's trials and 20.4% of Teco's trials were best fit by intercept. Only

Figure 11

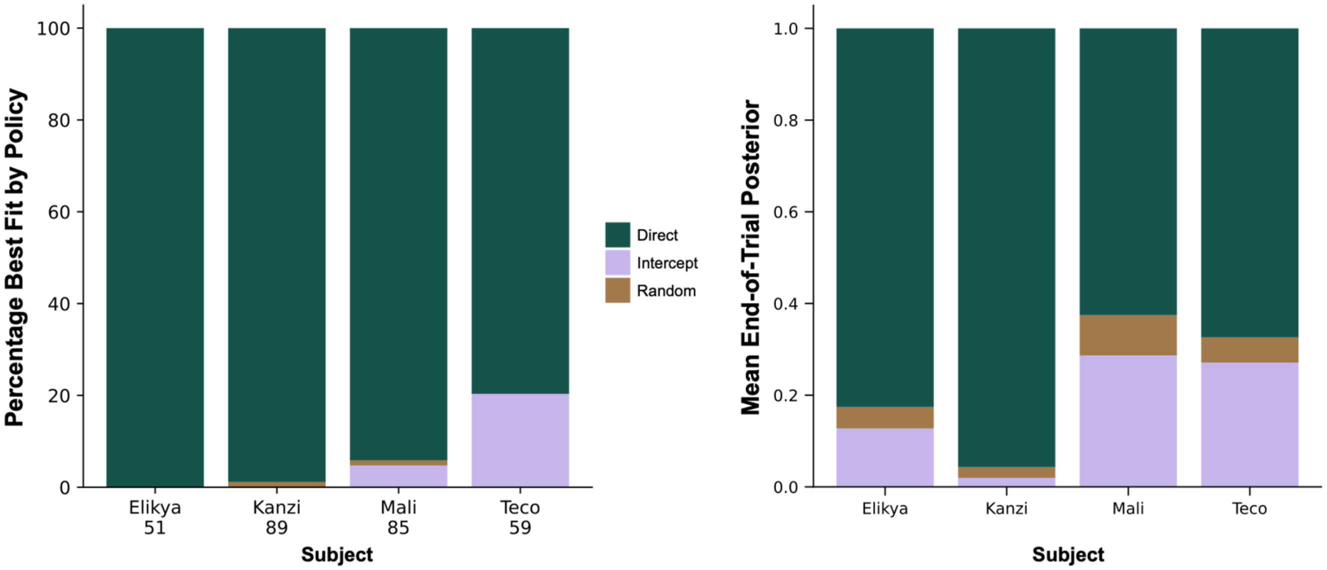
Chimpanzee Model-Based Analysis in Aggregate



Note. Left: The percentage of the trials best fit by each of the three model types for the seven chimpanzees. Numbers under their names indicate count of trials included in final analyses. Direct explains the majority of trials but there was some evidence for intercept in all subjects. Right: The average posterior at the end of each trial for the seven chimpanzees captures the uncertainty in strategy classification. See the online article for the color version of this figure.

Figure 12

Bonobo Model-Based Analysis in Aggregate



Note. Left: The percentage of the trials best fit by each of the three model types for the four bonobo subjects. Numbers under subject names indicate count of trials included in final analyses. Direct explains the majority of trials, but Teco had some trials that classified as using an intercept strategy. Right: The average posterior at the end of each trial for the four subjects captures the uncertainty in strategy classification. See the online article for the color version of this figure.

1.12% of Kanzi’s trials and 1.18% of Mali’s trials were best fit by random.

To examine whether our hand-built models effectively capture intercepting and direct chasing strategies as seen in subject behavior, we qualitatively analyzed the time steps across all subjects that give the highest likelihood for each model. Time steps scoring highly with direct policy reflect unambiguous direct chasing behavior; our analysis selected moments where intercepting was possible, but the participant still chose to chase the target directly (4/5 of top five time steps with highest direct likelihood; see Figure A7 in the online supplemental materials). Similarly, time steps scoring highly with intercept policy were good representations of intercept behavior (all five of top five): moments where there was an opportunity to directly chase the rabbit, but the participant chose the best intercepting direction.

Overall, our results suggest that subjects are capable of computing intercept trajectories for prey in VEs but rarely deployed this strategy in this task.

Discussion

Bonobos and chimpanzees learned to capture moving targets in a VE. For both species, static targets were initially easier to collect than moving ones; this effect remained throughout the experiment for bonobos. However, for chimpanzees, the analyses of their testing phase performance showed that they were equally successful with both target types. In the presence of obstacles, three chimpanzees and one bonobo reached success levels of over 80% with moving targets. Although one chimpanzee and all four bonobos were able to use both viewpoint modes, they were significantly more successful at collecting mobile prey and navigating around obstacles when the presentation was from a FP viewpoint as opposed to a top-down one. The other six chimpanzees failed to master the top-down view entirely. Finally, although we found some evidence of target interception, subjects mainly used a direct chasing strategy. Next, we discuss in greater detail each of these findings and their relation to each other.

It is unsurprising that catching rabbits was initially harder than collecting fruit. Not only had the subjects had more experience with fruit targets from previous studies, but catching rabbits required additional effort and concentration to track the target’s movement. But even though this was the first time that they had experienced virtual targets that moved away when approached, all subjects managed to adapt their responses to this animate and reactive prey, and in the testing stage, the chimpanzees’ performance showed no significant difference between fruit and rabbit trials. Moreover, four of seven chimpanzees and all four bonobos were successful in capturing the rabbit on their very first trial (Kilimi, Louis, and Liberius failed on the first trial but succeeded on their third, fourth, and fifth trials, respectively).

When designing the experiment, we expected that, in the condition where the subject began on the opposite side of the arena from the target, trials containing an obstacle would be more difficult to succeed in than trials without one. To achieve high levels of success in these trials, subjects must have some understanding of the solidity of the obstacles, and that they cannot pass through them and therefore cannot reach the target via the shortest, most direct path, but instead must go around. This navigation will often entail losing sight of the target temporarily, requiring the subject to apply object permanence to virtual objects (Call, 2001). On the other hand, in trials where the target was on the same side of the arena as the subject, the presence or absence of an obstacle should be irrelevant.

We did not formulate specific predictions about which of the two obstacles would prove harder in FP mode, for they each posed different complications. We expected trials with the lake to be difficult because subjects would be able to see the target across the lake, and so might want to approach it directly; success would require the subject to inhibit touching the visible target and turn away from it to walk around the obstacle. Trials with the forest would be difficult for precisely the opposite reason: The obstacle would block the subject's view of the target, meaning they must extrapolate from experience in previous trials to comprehend where the target was located. In overhead mode, however, the lake and the forest were functionally equivalent, so we expected to see no difference in subjects' success across these conditions.

These expectations were borne out in our results. In the analysis of the bonobo test results, and in the analysis of the FP chimpanzee test results, the obstacle/start relationship interaction was significant: When subjects began opposite the target with no obstacle, they were much more successful than in lake or forest trials. But in trials where the subjects began on the same side as the target, success levels were almost the same in both the presence and absence of obstacles. Interestingly, however, in the bonobo data, we can see that when we consider trials with no obstacle, subjects were slightly more successful in opposite than in same trials. One explanation for this may be as follows: When the subject begins a trial on the same side of the arena as the target, the target may initially be out of sight—since the FP viewpoint does not afford a 360-degree, panoramic view of the arena. So although in these trials the target is nearby and therefore easy to access, the subject may have to tap on the side of the screen and turn themselves in place in order to bring the target into view. In contrast, in no-obstacle opposite trials, although the target is further away, it is always in sight from the very beginning of the trial.

It may be the case that in some trials, subjects were able to succeed not because they understood how to circumnavigate the obstacles, but because the time they were allowed per trial was sufficient to enable them to reach the target simply by inching around the edge of the obstacle rather than showing an effort to avoid it altogether. It is true that certain subjects, such as Qafzeh and Velu, appeared to have difficulty comprehending the physical impermeability of the obstacles, and would appear to continuously tap on them as if they could walk through them, ending up getting around them merely through imprecisions in their touches. This can be observed by looking at their data paths through the environment (Figure 13A and 13B): On some trials, they keep very closely to the contours of the obstacles instead of taking an avoidant path around them. However, in other cases, they do give the obstacles a wider berth, as do other individuals (Figure 13C–13F).

This may tell us that apes do not enter the VE with a preconfigured expectation of the "physical" properties of objects therein—such as an understanding that they cannot cross a virtual lake, just as they cannot cross a real body of water—but may need to learn this over time.

However, it is also possible that subjects keeping close to the obstacles were doing so on purpose, using them as guides to help them find their way through the arena and avoid accidentally getting turned around. In the absence of obvious landmarks that can guide their orientation, this would be a valid strategy, particularly in forest trials where the target is not in view. Further, directed work would be required to tease apart these possibilities. For examples of failed and successful FP and overhead trials, see Supplemental Videos 1–3.

Another important dimension that modulated subjects' responses was the viewpoint mode. In the analysis of the chimpanzee test results with both FP and overhead trials (recall that this analysis contained data from Velu only), we saw a significant interaction between start relationship and viewpoint. However, these relationships were not entirely in the directions we had predicted. We expected overhead trials on average to be easier than FP trials in cases where the subject and target started on opposite sides, because if there was an obstacle, it might block the subject's view in FP but not in overhead mode; however, we saw the reverse of this. In opposite trials, Velu was more successful in FP than in overhead trials, while in same trials he reached almost perfect success in both viewpoint modes.

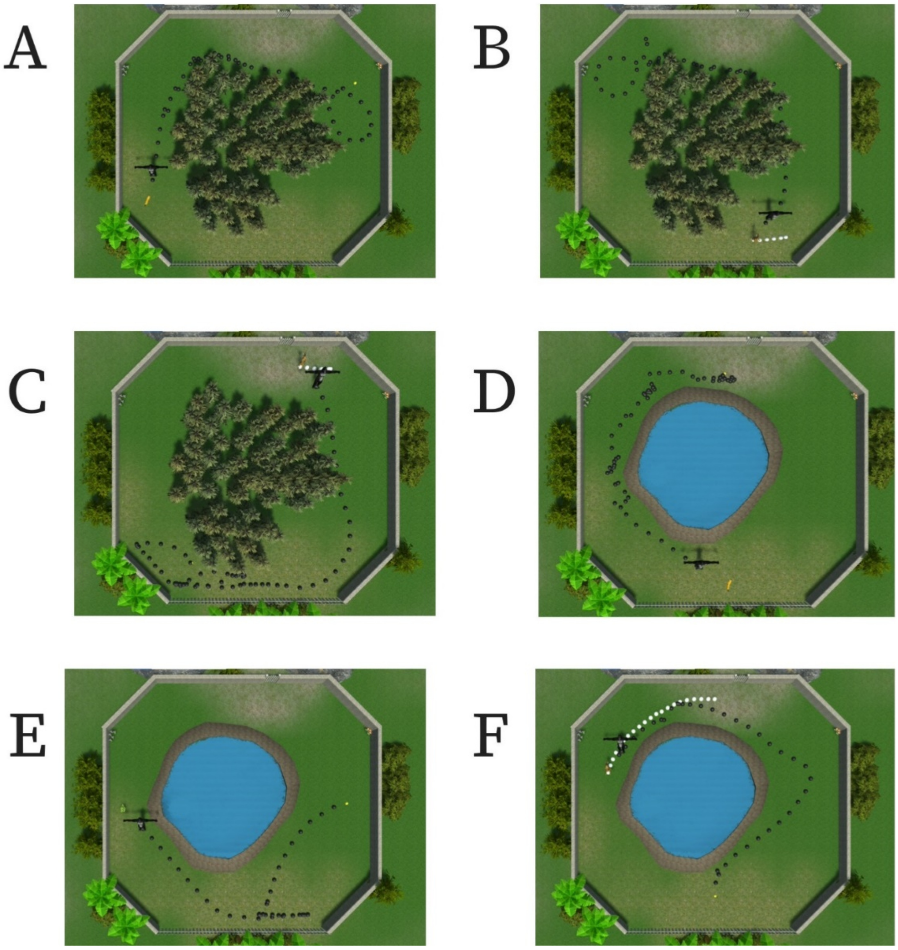
This likely reflects the fact that all chimpanzees—Velu included—found the overhead viewpoint far more difficult than FP, which is why Velu was the only chimpanzee to receive overhead trials in the testing phase. The bonobos also found overhead more difficult than FP, as reflected by the fact that viewpoint was a significant and negative predictor of performance in both the training and testing analyses.

Why might this be? Although the overhead view affords an unobstructed view of the entire arena, it is far less immersive and more abstract: The subject observes their avatar moving around from a top-down view, rather than experiencing the realistic changes in perspective that occur in FP trials. This may make it harder for the subject to situate themselves within the environment, to understand the relations between the location of their avatar and the target, and to avoid bumping into obstacles. Subjects may have also failed to recognize that the ape avatar represented themselves and their own positioning within the environment, reflected by the fact that some appeared to tap on their own avatar as if it were the target (see Supplemental Video 3). This observation lends strong support to the idea we set out in the introduction that the use of 3D, first-person VEs would open up opportunities for the study of a greater variety of aspects of cognition than have thus far been investigated using 2D, bird's-eye view VE presentations. It is notable that subjects in this study reached high rates of successfully catching the rabbit in the FP condition after only a few dozen trials. In the only other study to test the ability of a great ape to approach moving targets in VE (Iversen & Matsuzawa, 2003) the virtual presentation was a flat, top-down view; the target was a colored circle that moved around the screen in a predictable pattern, with no obstacles between it and the subject's cursor. In this situation, subjects required several hundred trials to become proficient at chasing and intercepting the target. By virtue of potentially feeling more realistic and immersive, 3D, FP environments could allow primate subjects to engage more deeply in the task at hand, rendering cognitive tasks more valid and less abstract as they tap into subjects' real-world responses to the stimuli that are presented.

Using our computational agent-based analyses, we found that for both chimpanzees and bonobos, direct chase was the favored strategy for catching prey. For the chimpanzees, a smaller proportion of catching events could be attributed to the use of an interception strategy; for bonobos, there were only a few examples of this. These results indicate that while both species were capable of anticipating and plotting courses to intercept moving prey, they chose mainly to chase. However, note that this experiment was not designed to elicit interception behavior: The rabbits were slow-moving, and only ran a short distance before pausing and choosing (randomly) another direction in which to run, meaning that a direct chase strategy was sufficient to capture them—and indeed, successful interception would often be impossible. It is an open question, therefore, whether with faster prey that make a chase strategy

Figure 13

Data Paths From Randomly Selected Trials Featuring an Obstacle in Which the Subject Began on the Opposite Side of the Arena From the Target



Note. Black dots show the path taken by the subject; white dots show the path taken by the rabbit prey. The single yellow/light gray dot denotes player’s starting position; the virtual ape denotes player’s final position. (A) A forest trial undertaken by Qafzeh, in which the target is a banana. (B) A forest trial by Velu, with a rabbit target. (C) A forest trial by Qafzeh, with a rabbit target. (D) A lake trial taken by Velu, with a banana target. (E) A forest trial with a rabbit target undertaken by Eva. (F) A lake trial taken by Kanzi, with a rabbit target. See the online article for the color version of this figure.

moot, chimpanzees and bonobos would develop interception strategies in VEs.

Does this mean that our results show good evidence of chimpanzees and bonobos navigating around virtual obstacles in the same way they navigate obstacles in the real world? Not necessarily, but we would like to highlight two things. First, our subjects have far more limited experience navigating the VE than the real world, which they have done their entire lives. Based on this differential experience it is therefore unrealistic to expect that they would behave in identical ways in both settings. Second, we are not claiming that apes’ behavior in VE can be taken as a one-to-one mapping from their behavior in the real world. However, our contention is that the way apes respond to the VE differs in important ways from the way they interact with more traditional computer-based tasks. Besides the advantage in speed of acquisition noted earlier, subjects learn to touch the screen not just to select stimuli but to seek information by altering their field of view and using the new information, such as landmarks, to locate targets (see Allritz et al., 2022). Moreover, their turning behavior in other VE foraging tasks suggests that chimpanzees are capable of encoding the position of targets egocentrically to later retrieve them using the shortest turn possible, after they have disappeared from sight (Koopman et al., 2024).

Whether nonhuman primates experience and perceive these VEs in the same way that we do remains an open question. Although images in VE are by default 2D, humans perceive and interact with them as if they are 3D spaces populated by objects, geometry, and topography reflective of the physical properties of the real world (Dolins et al., 2014, 2017). It is ultimately impossible to verify that nonhuman primates also experience VEs in this way; however, as experiments of this kind become more common, and as primates continue to demonstrate navigational performance in VEs that mirrors that of humans (such as in Dolins et al., 2014) and resembles behavior that would be expected in physical environments (as seen in Washburn & Astur, 2003), evidence is building up that points to the affirmative. For example, one study (Imura & Tomonaga, 2007) showed that chimpanzees' visual search patterns in response to virtual objects are comparable to those of humans, indicating strong parallels between chimpanzees' and humans' perception of 2D visuospatial information (Dolins et al., 2014, 2017).

One could argue that although the environments we presented were designed to look 3D, they still lack photorealistic verisimilitude. Nevertheless, researchers have reported that the visual fidelity of the images is less important to the experience than one might expect (Waller et al., 2001), and that the way in which images change as the subject moves around in the VE is enough to render realistic feelings of locomotion and orientation through depth cues and optical flow (Regan & Price, 1994). Another potential issue is the relatively narrow field of view that is achievable on a flat computer monitor (Dolins et al., 2017). However, it has been argued that VE presentation on flat monitors is sufficient to create immersion for animals with stereovision and front-facing eyes, like primates (while it might pose more of an issue for animals whose eyes are more lateral, such as birds) (Doucet et al., 2016). In addition, researchers have argued that the FP aspect of these environments, and the concomitant inducement to imagine oneself as seeing through the virtual avatar's eyes—combined with the visual cues just discussed, and evocative auditory cues such as the sound of footsteps—have the potential to create conditions in the subject that are strongly reminiscent of real-world experiences (Mitchell, 2002); after all, "imagination is a powerful aspect of all cognition" (Dolins et al., 2017, p. 99).

Future Directions

This study could form the backdrop for several further experiments investigating how great apes hunt moving prey. For example, do they adapt their hunting strategies according to the prey's behavior? Will their use of anticipation and interception increase when confronted with prey that are too fast to catch by chasing? One matter of debate is the extent to which chimpanzee and bonobo group hunts represent cooperative activities as opposed to individuals working independently but in parallel (Boesch, 1994, 2002; Gilby & Connor, 2010; Melis & Warneken, 2016; Tomasello et al., 2005). This question has not been directly investigated with captive chimpanzees due to the obvious logistical and ethical issues present, but it could be examined in VE by presenting subjects with hunting tasks in which they must work together with virtual cooperators in various ways.

Additionally, since ape subjects can rapidly learn to respond efficiently to virtual agents that are animate and reactive, VE could present itself as a valid paradigm for the study of ape social cognition as well as spatial. Future studies could investigate topics such as social learning and theory of mind in virtual situations. To tap into subjects' behavioral responses to the fullest extent, future VE studies should focus on FP presentations that are designed to be as immersive and as realistic as possible.

Conclusion

This study was motivated by two considerations. First, that there remains much that we do not know about the cognitive underpinnings of great ape foraging and hunting and the capacities and strategies that allow them to overcome the challenges that are associated with these activities. These challenges include the need for robust working memory, the possible need to form dynamic representations of prey animals, and the need for long-distance navigational abilities. Second, that part of the reason for our limited understanding of the above is due to the comparative difficulty of exploring these questions both in the field and in traditional experiments. For this reason, VEs appeared to be an ideal paradigm with which investigations on this topic could be continued and expanded. Our study combined the twin aims of validating the above idea, while also providing a first step in this direction.

Using a combination of traditional analysis and computational modeling, we found that both chimpanzees and bonobos can rapidly learn to catch moving virtual prey even in the presence of differing viewpoints, starting positions, and obstacles (although they may require further training to fully appreciate the "solidity" of obstacles and endeavor from the outset to walk around rather than through them). We found that they are capable of occasionally intercepting targets by anticipating their future locations, although they favor a direct chasing strategy. Our work, when combined with previous research, shows promising progress in the field of VE paradigms. But there is still much to be done in confirming the above, such as studies in which apes complete the same tasks in the same environment in both a real-world and a virtual context, to identify whether their behavior in one maps across to the other. In all, we feel that this study confirms the original premise that VE paradigms, when carefully designed, can be employed to provide a compromise between traditional field and experimental methodologies.

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