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Training primates to forage in virtual 3D environments

Emma Suvi McEwen [a,*,1,2], Matthias Allritz [b,1], Josep Call [a], Sarah E. Koopman [a], Emilie Rapport Munro [a], Cristóbal J. Bottero Cantuarias [b], Charles R. Menzel [c], Francine L. Dolins [d], Karline R.L. Janmaat [e,f,g], Kenneth Schweller [h]

[a] School of Psychology and Neuroscience, University of St Andrews, UK
[b] Department of Comparative Cultural Psychology, Max Planck Institute for Evolutionary Anthropology, Germany
[c] Language Research Center, Georgia State University, USA
[d] Department of Behavioral Sciences, University of Michigan, Dearborn, USA
[e] Evolutionary and Population Biology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Netherlands
[f] Department of Cognitive Psychology, Leiden University, Netherlands
[g] ARTIS Amsterdam Royal Zoo, Amsterdam, Netherlands
[h] Ape Cognition and Conservation Initiative, Des Moines, IA, USA

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ABSTRACT

Virtual environment software is increasingly being employed as a non-invasive method in primate cognition research. Familiar and novel stimuli can be presented in new ways, opening the door to studying aspects of cognition in captivity which previously may not have been feasible. Despite the increased complexity of visual input compared to more traditional computerised studies, several groups of captive primates have now been trained to navigate virtual three-dimensional environments. Here, we outline a method for training primates to use a computerised virtual foraging task presented on a touchscreen. We document how to tailor this method to groups facing different training challenges. We present data from three groups: touchscreen-experienced chimpanzees (*Pan troglodytes*), touchscreen-naïve orang-utans (*Pongo abelii*), and chimpanzees tested in a group setting. Subjects from all groups mastered basic navigation challenges with relative ease (some in as little as 16 days), setting them up for systematic studies of primate cognition within virtual environments. The training method we present is flexible, yet structured, and we encourage other researchers to adapt it to implement virtual environment research with more individuals and across more species.

1. Introduction

Since the turn of the century, virtual environment (VE) technology has been used to study animal behaviour (for a review, see Naik et al., 2020). In VE tasks, subjects are presented with computer generated stimuli aiming to simulate a three-dimensional (3D) space. The tasks are often controlled by subjects' interactions or movements (feedback-based), meaning that the subjects themselves decide when, and in which direction, to move (Dombeck and Reiser, 2012). VE research has the potential to make novel kinds of experimental studies of animal behaviour possible, for example, due to increased realism in presenting ecologically relevant stimuli, as well as the possibility to increase available navigation space compared to the space available in real life in captive environments (for example, Dolins et al., 2017, Allritz et al., 2022). Whilst many studies using VEs currently focus on validation (that is, demonstrating that findings from real life studies can be replicated in analogous VE situations), researchers have also suggested future applications of VEs for studying aspects of animal cognition that would currently be difficult or impossible to study with traditional methods. This includes the study of spatial learning and cognitive maps in large scale environments, while retaining full experimental control over environmental layout and learning history (Allritz et al., 2022; Koopman et al., in press), the evolution of language (Nölle and Peeters, 2023), and the study of social behaviour in response to virtual conspecifics, for example, in the context of collective behaviour (Stowers et al., 2017), or competition and cooperation (Allritz et al., 2022, Rapport Munro et al.,

* Corresponding author.
E-mail address: esm7@st-andrews.ac.uk (E.S. McEwen).
[1] ESM and MA contributed equally to this manuscript.
[2] https://orcid.org/0000-0002-3886-0255

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in press).

Regarding validation, in neuroscience, many advances have been made in recent years in demonstrating similarities between real life navigation and navigation in virtual worlds. In free-moving mice, *Drosophila*, and zebrafish, immersive virtual stimuli have elicited 'naturalistic' behavioural responses, such as height aversion and movement trajectories (Stowers et al., 2017). Similarities in responses to virtual and real life environments have also been found on a neural level. Place cell activity comparable to that seen in real life tasks has been found in rodents walking on a spherical treadmill and viewing a VE on a screen (Harvey et al., 2009). In VE tasks viewed through polarised lenses, place-related neural responses and simple maze navigation abilities have been shown in monkeys (Hori et al., 2005; Wirth et al., 2017; Sato et al., 2004). Less immersive desktop VEs showing 3D environments in two-dimensions (2D) have also been used to study eye movements in rhesus macaques (Corrigan et al., 2017).

Recently, VEs have been implemented as a non-invasive method of studying cognition in free-moving (that is, without forced restraint) non-human primates (hereafter, primates; Washburn and Astur, 2003; Dolins et al., 2014; Allritz et al., 2022). Dolins and colleagues (2014) presented chimpanzees with interactive 3D maze environments on computer screens to investigate their ability to use virtual landmarks as associative cues. The apes used joysticks to direct the movement of an agent through these mazes (on a voluntary basis). Chimpanzees were able to learn to use virtual landmarks to travel to reward locations and demonstrated, in one case, more efficient routes than human participants (see Dolins et al., 2017 for a description of the training methods employed for the sample of apes in Dolins et al., 2014). More recently, with reference to findings from real life navigation, Allritz and colleagues investigated the flexibility of virtual associative landmark use in chimpanzees, and found that chimpanzees could locate hidden virtual food in a more naturalistic, open-space VE presented on a touchscreen (Allritz et al., 2022). Chimpanzees learnt, over the course of just 14–18 days of testing, to associate a landmark (a large tree) with the presence of nearby virtual food items. The chimpanzees could also navigate to this landmark when starting from varying positions within the arena, including cases in which the landmark was not visible at the beginning of the trial. In some conditions, the chimpanzees increased their path efficiency over time, exhibiting behavioural signatures of real-world navigation. Subjects also very quickly learned the location of a second landmark tree that only sometimes bore fruit, often checked both potential virtual food locations in a sequential manner, and became more successful over time. A recent study by Koopman and colleagues explored whether chimpanzees (many of whom had participated in the study by Allritz et al., 2022) would use the VE application controls to turn the agent towards desired objects in efficient ways. The authors' analysis revealed that, particularly in later trials, five of the six chimpanzees turned the agent in an efficient manner, effectively demonstrating an ability that the authors likened to object permanence in virtual space (Koopman et al., in press). That is, when the chimpanzees had directed the invisible first-person virtual agent to move past a piece of virtual fruit so that it was no longer in their field of view towards the left or right side of the screen, they would then turn the agent right or left, respectively, minimizing the amount of turning required to re-orient towards the virtual fruit they had just passed. Finally, Rapport Munro and colleagues (in press) tested whether a different group of seven chimpanzees and a group of four bonobos would be able to navigate similar virtual environments to direct the movement of the virtual agent to collide with a moving target stimulus (resembling mobile prey), expanding the use of virtual environments to study aspects of social cognition. Chimpanzees and bonobos in this study directed first-person virtual agents to successfully chase and catch virtual moving rabbits and were considerably more successful when this challenge was presented in a first-person 3D view (with an invisible agent) than when guiding a visible virtual agent to catch the same prey presented in a 2D overhead view version of the task (Rapport Munro et al., in press). In sum, research has shown that 3D VE tasks are a viable method of studying primate cognition.

VEs can be useful tools in primate cognition research; however, as with many methods, they require some basic training before experimental implementation. To this end, we have developed a replicable training method for great apes to learn to navigate a virtual foraging environment, that many subjects have progressed through quickly. In this set of tasks, apes are presented with a VE that they could navigate through to collect virtual food items via a touchscreen interface. During the development of this training method, we were faced with two main challenges: subjects who had no previous touchscreen experience, and subjects who participated in research in a group setting. In this article, we outline our training methods, describe the training with touchscreen experienced chimpanzees who could be tested individually, and detail how the training methods were adapted to address training challenges. Finally, we discuss implications for future training efforts. Consequently, the aim of this article is two-fold. Our first aim is to offer a reliable method for training the basic gameplay mechanics of the freely available VE software APExplorer (Schweller et al., 2022; OSF link: osf.io/sx5pm). Our second aim is to document how three groups of apes performed with this training method in different testing contexts. We are mindful that the adoption of new methods is time consuming and costly, and we aim to facilitate the use of VEs with larger samples and diverse groups of primates (and more taxa), including those who are touchscreen-naïve and tested in group settings. These two challenges may represent the conditions in many settings where researchers wish to expand their toolset of methods to touchscreen VE tasks.

2. Method

2.1. Subjects

We trained a total of 26 subjects belonging to three different groups (see demographic information in supplementary Table S1). Participation was entirely voluntary and non-invasive, and subjects were never food- or water-deprived. Water was available ad libitum both in enclosures and testing rooms. All research and husbandry complied with the European Association of Zoos and Aquaria (EAZA) and the World Association of Zoos and Aquariums (WAZA) regulations. Research in Edinburgh was approved by the Budongo Research Unit (BRU) committee, consisting of the Zoo Research Liaison Officer, the Scientific Director, and the Research Coordinator. Research in Leipzig was approved by the Wolfgang Köhler Primate Research Center (WKPRC) committee, composed of the director of WKPRC, the research coordinator, the head keeper of great ape husbandry, and the zoo veterinarian. This research was also approved by the School of Psychology and Neuroscience ethics committee at the University of St Andrews.

2.1.1. Leipzig chimpanzees

Five chimpanzees housed in the WKPRC in Leipzig Zoo participated in the training described in this article (3 females, 2 males; age range = 4.9 – 44.3 years, mean age = 29.2 years), 4 of whom already had touchscreen experience with 2D tasks (although for one subject, Daza, the touchscreen experience was limited to training in a simple discrimination task, and not participation in a touchscreen experiment). One subject, Azibo, had no prior touchscreen experience. This group of chimpanzees was trained primarily from October 2021 to February 2022 (see Figure S1). Prior to this, in October 2019, Daza, Robert, and Azibo received a small number of sessions (Daza: 8, Azibo: 2, Robert: 2), which are included in the data presented here. The individuals belonged to two separate housing groups at Leipzig Zoo, which, at the time when data collection began, consisted of 21 individuals (14 females, 7 males) and 6 individuals (5 females, 1 male), respectively. Chimpanzees in the large social group were tested for a total of 34 days (all Leipzig chimpanzees in this article except for Daza, who was housed in the smaller social group of chimpanzees in Leipzig and was tested for 31 days). In Leipzig, individuals could be given the opportunity to briefly separate themselves from the group for cognitive testing (typically between 5 and 20 minutes). For those individuals who participate, the doors to the enclosure are closed during testing to minimize distraction that may otherwise happen in a zoo (for example, lower ranking individuals being displaced while they are attempting to participate). If individuals initially engage with the task and then signal that they want to end participation, either via approximately 3 minutes of inactivity or other known, clear signals (such as moving towards or holding onto the sliding door), they are let out of the testing room. Based on a number of considerations, including the available testing time and prior experience with separation for testing, 5 chimpanzees were recruited for this training period.

2.1.2. Leipzig Orang-utans

Six orang-utans housed in the WKPRC in Leipzig Zoo participated in the training described in this article (5 females, 1 male; age range = 5.9 – 31.3 years, mean age = 19.4 years). This group was initially trained from October 2019 to March 2020, at a time when all 5 orang-utans who participated were completely inexperienced with using touchscreens. Then, after an extended hiatus, members of the housing group were again trained from June to August 2023 (see Figure S1), at which point one orang-utan (male Suaq) had moved to a different zoo (meaning that Suaq's data collection ended in 2020), and another (female Sari) had become old enough to participate in research (Sari had not participated in the training prior to the testing break). During the testing break, all orang-utans had gained initial or additional touchscreen experience with a 2D task with static images. The individuals belonged to a single housing group of orang-utans at Leipzig Zoo, that consisted of 8 individuals (5 females, 3 males) at the time when data collection began and of 7 individuals (6 females, 1 male) after the hiatus. This group was tested for a total of 38 days. Testing procedures were identical to those described for Leipzig-housed chimpanzees (individuals separated themselves for testing, as with the Leipzig chimpanzees). During both data collection periods, we aimed to recruit all orang-utans in the group for testing, with the exception of adult male Bimbo, who was excluded for safety considerations regarding the testing equipment, as well as individuals who at the time of data collection were too young for participation.

2.1.3. Edinburgh Chimpanzees

Fifteen Edinburgh-housed chimpanzees participated in the training described in this article (7 females, 8 males; age range = 2.2 – 44.3 years, mean age = 27.7 years). Based on the published record of touchscreen studies from Edinburgh Zoo (Herrelko, 2011; Herrelko et al., 2012; Ravignani and Sonnweber, 2017; Sonnweber et al., 2015; Wallace et al., 2017; Altschul et al., 2017), and our own unpublished records of initial touchscreen testing in Edinburgh before VE training began, at least 13 of the Edinburgh chimpanzees (5 females, 8 males; all subjects included in this manuscript except for Masindi and Heleen) had some level of touchscreen experience with traditional tasks with 2D images or shapes when the VE training began. The chimpanzee group at Edinburgh Zoo, at the time when data collection began, consisted of 16 individuals (8 females, 8 males). Unlike Leipzig-housed apes, Edinburgh-housed chimpanzees were tested in a group setting. All testing in Edinburgh Zoo was conducted in the BRU, which is adjacent to the apes' main enclosure. All apes can enter and leave this area at any time during the 4-hour daily testing period. Individuals decide freely whether and for how long to participate. Training began in June 2019 and has continued since (see Figure S1), with breaks during the beginning of the COVID-19 outbreak (March to August 2020 and January to April 2021). Chimpanzees in this group were tested for a total of 320 days. The data presented here include training conducted before August 2023.

2.2. Materials

2.2.1. The APExplorer virtual environment program

The virtual foraging game (APExplorer_3D) was programmed in C# with the Unity3D game engine. A free version of the software can be downloaded at osf.io/sx5pm (Schweller et al., 2022), and the files required to run the protocol described in this paper can be found in the following OSF repository: https://osf.io/wqzj3/?view_only=735ebc1bb6dd4255963743ded64e922e. Details of how to set-up the software to run the training protocol in this article can be found in the supplementary materials. During training, great apes interact with a simple 100 m squared VE that consists of a grassed area with a lake, rocks, trees, and virtual fruit. The environment is viewed in a first-person perspective and consists of 3D objects presented in 2D, as in many video games. The apes move an agent (from first-person point of view) around the environment by touching the screen and 'collecting' virtual fruit, for which they are rewarded with a piece of the equivalent real fruit. Each time contact is made with the screen, this is registered as a touch to which the program responds, either by (1) the virtual agent moving towards the touch location, or (2) by rotating the agent's centre of field of view towards the touched location. If the agent makes contact with a virtual piece of food, the virtual food is 'collected' (see below). In our testing, the experimenter manually gives the fruit rewards to the subjects, but the application also gives the option of using an automated food dispenser (see the APExplorer user guide for information about setting this up; Schweller et al., 2022).

When a location in the virtual world on the screen (other than the sky) is touched, the agent walks indefinitely in this direction until the agent either arrives at the touched location, until they arrive at a virtual fruit or an object (defined as solid or not walkable, such as rocks, trees, walls, and water surfaces), or until the subject changes the agent's trajectory or bearing with further input. The walking bout length per screen touch is a parameter that can be set by the experimenter within APExplorer. To allow for orienting on the spot without changing location, when the bottom two corners of the screen are touched, the agent rotates on the spot (see Fig. 1 for details). As the virtual agent moves around the arena, footstep noises are sounded. When a virtual fruit is collected, a reward sound ("tadaa") is played, the virtual fruit briefly rises into the air before disappearing, and a piece of real food is delivered to the ape.

The APExplorer_3D app provides the option to choose different items for subjects to collect in the VE task. For our training purposes, we selected virtual apples, grapes, and bananas for the orang-utans and apples, grapes, peanuts, bananas, and blueberries for the chimpanzees.

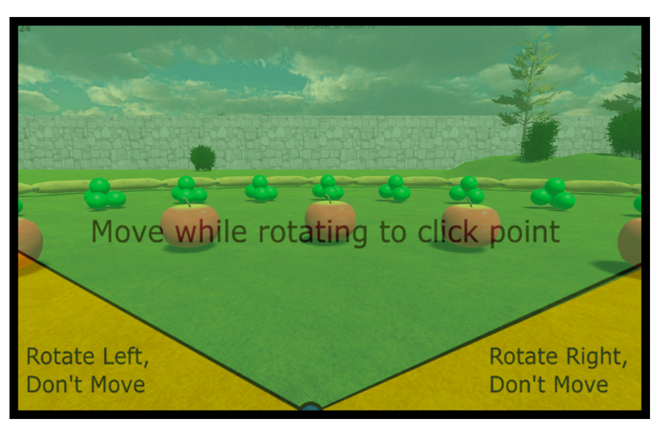

Fig. 1. Depiction of the way in which the screen is divided (approximation) into areas that when touched result in the agent moving to the location (green), and areas that when touched result in the agent turning on the spot (yellow). Angles that define areas in this illustration approximate, but may not exactly match, angles implemented in the software.

The app also allows for different simulated camera views, for example, behind the agent's head, or behind the agent such that its whole body is in view. For our training, we selected a pure first-person point of view, so that the agent's body and head are not visible to subjects.

The environment contains some items that act as obstacles and must be circumvented in order to collect all virtual fruit. When the agent walks into these obstacles, or into one of the four walls surrounding the arena, it bounces back slightly. Thus, subjects receive continuous feedback as engaging with the touchscreen results in a continuous stream of movement and sound, even when the subject is not immediately rewarded. The absence of sound signals that the agent has come to a rest, even when the subject is temporarily not looking at the screen. The freedom to roam anywhere in the open environment sets the current work apart from previous work with virtual mazes. A trial is finished either when a prespecified number of virtual fruits are collected, when a time limit is reached, or when a subject chooses to no longer engage with the task.

2.2.2. Apparatus

The touchscreen setup consisted of a solid metal frame that housed both an infrared touch frame and a transparent acrylic panel. Subjects could touch this acrylic panel, through which they could see a computer monitor that was mounted behind the panel, and that displayed the VE game (Fig. 2 shows the set-up from the experimenter's perspective, the supplementary video shows the apes' perspective). The location touched on the acrylic panel corresponded to the locations on the monitor mounted behind it. The setups had different dimensions, ranging from 19'' to 27'' screen diagonals, depending on site and time of data collection (for details and models, see supplementary materials). Two speakers were located just outside of the ape testing area in the experimenter area, to provide auditory feedback throughout the task. Fig. 2 shows an example of the set-up for Leipzig-housed chimpanzees. The other groups were tested with very similar set-ups. In Edinburgh, a second, smaller monitor was connected to a camera that filmed subjects from behind while using the touchscreen, allowing the experimenter to quickly identify subjects whenever they began engaging with the screen. We chose touchscreens as the interface with which subjects would provide their input for agent navigation out of convenience. Unlike in some previous joystick-based studies of virtual environment navigation by chimpanzees, that were carried out at the Language Research Center at Georgia State University (Dolins et al., 2014), in the two sites that participated in this investigation (Leipzig Zoo and Edinburgh Zoo), studies using joysticks had never been carried out before, whereas touchscreen infrastructure was already available, and many subjects had already used touchscreens.

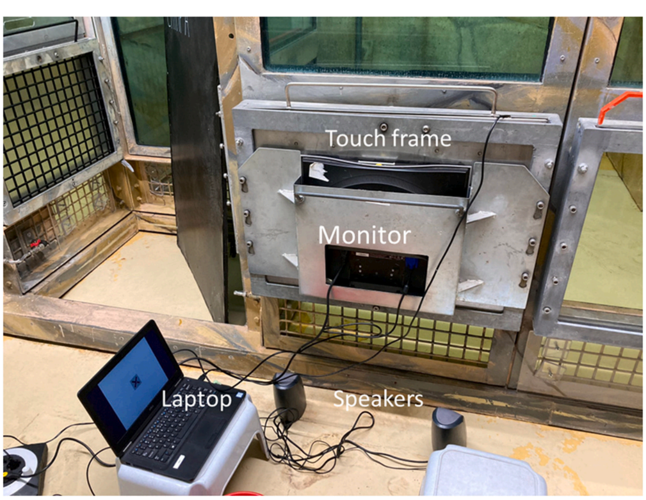

Fig. 2. Touchscreen testing set-up for Leipzig chimpanzees.

2.3. Procedure

2.3.1. Development of the training procedure

Our first approach to training the chimpanzees with this program was based on our previous success in training a different group of chimpanzees in Leipzig ("original Leipzig chimpanzee" group) who had considerable prior touchscreen experience (see Allritz et al., 2022). With the original Leipzig chimpanzee group (whose training is not presented in this article), we began with a training stage resembling Stage 4 of the current protocol ("medium scatter", the second-most challenging stage, described in Table 2), but with more flexible decision-making regarding experimenter intervention. During this training period, the experimenter simply intervened when they deemed it necessary and allowed subjects to progress when they no longer needed assistance, rather than having the set times to wait before intervening and systematically increasing these waiting periods, as we describe below. When we began training new subjects (those in this article), we realised that we needed an incremental training regime that started with more basic training, as well as more specific criteria for monitoring success on each training step.

2.3.1.1. Inexperienced subjects: Incremental training. In October 2019, a few months before the beginning of the COVID-19 pandemic, we began training the group of orang-utans, housed at Leipzig Zoo, Germany. Our training aims were the same as those outlined above: subjects should learn how to interact with the touchscreen to make the invisible first-person agent move and turn on the spot for orienting, and to differentiate virtual food from virtual non-food objects for efficient foraging. Unlike the original Leipzig chimpanzees, the orang-utans had never used touchscreens before.

Traditionally, although this is rarely documented in detail (but see Schmitt, 2019 and Martin et al., 2022), touchscreen-training primates includes shaping procedures in which static (and in some cases, moving) geometric shapes or 2D pictures of different sizes are presented to the subject on a screen. Touching these virtual items then results in real food rewards. As subjects progress, these items, or the touch-responsive area around them, are made smaller, and/or they change locations across trials to help subjects to learn to attend to the full display and to use precise touches. Such basic touchscreen training is traditionally then followed by more specific (and usually well-documented) training for the relevant paradigm and research question at hand (for example, matching-to-sample: Martin et al., 2011; Kawaguchi et al., 2020; discrimination learning: Allritz et al., 2016; Gao et al., 2018; or serial learning: Allritz et al., 2021; Beran et al., 2004).

Because of the encouraging fast training progress that we had seen with the original Leipzig chimpanzees, we decided to incorporate the earliest forms of touchscreen training for the orang-utans (for example, learning to touch and attend to the touchscreen in the first place) into the VE navigation training procedure. We followed the same principles that are used in training primates to use joysticks (Rumbaugh et al., 1989; Evans et al., 2008) and touchscreens (Schmitt, 2019) as input devices in traditional 2D computer-controlled tasks. At first, a single, or a small number, of manual contacts with the input device should result in a reward, with a large tolerance regarding which location on the input device the subject needs to touch. Then, as the subject builds up motivation to engage with the input device, the task slowly becomes more challenging, with smaller targets and longer periods between rewards. Thus, in the first stage of this training procedure (Stage 1 "concentric circles" in Tables 1 and 2, and Fig. 3, note that the targets in the birds-eye-view images within Figs. 3–7 are best viewed on a high-resolution computer screen) the invisible first-person agent starts surrounded by three concentric circles of virtual food. Touching the monitor in any location will in most cases set the agent on a straight course towards a reward. After the first on-screen fruit has been collected by the agent (and the subject is rewarded), the subject, by

Table 1
Overview of the different stages of VE training.

Stage	Overview
1: Concentric circles (Fig. 3)	The agent is surrounded by three circles of virtual fruit
2: Concentric circles with a gap (Fig. 4)	As above, with a gap in the virtual fruit circles at the agent's start view line of vision
3: Small Scatter (Fig. 5)	The agent is surrounded by virtual fruit, slightly further away and more sporadic than previously. Stages 3 A, 3B, 3 C refer to different levels of difficulty based on how long the experimenter waits before helping.
4: Medium Scatter (Fig. 6)	Virtual fruit is scattered around the central part of the arena
5: Large scatter (Fig. 7)	Virtual fruit is scattered all around the arena

touching the monitor again, is likely to set the agent on a course towards another virtual fruit. That is, either, if the subject touches the screen in the centre, the agent will move towards a piece of virtual fruit in one of the outer circles, or, if the subject touches the screen on the side, the agent will move towards one of the nearby virtual fruits from the same circle. As not every single touch to the screen will result in reward, the experimenter continuously encourages the subject verbally or by gently knocking against the back of the touchscreen setup to continue engaging with the touchscreen. The pass criterion for this stage, which requires subjects to collect three virtual fruits within a time limit for a minimum number of trials, ensures that by the time they are promoted they are motivated to touch the screen frequently and in quick succession. The pass criteria for all training stages are given in Table 2.

In the second stage (Stage 2, or "concentric circles with a gap" in Tables 1 and 2, and Fig. 4), the invisible first-person agent starts in the centre of a similar array of three concentric circles of virtual fruit. However, now the virtual fruits that in Stage 1 were in the centre of the agent's field of view at the trial start, have been removed from all three circles. This layout was partially inspired by joystick training in 2D formats used in Evans et al. (2008) with capuchin monkeys. This means that, to collect virtual fruit, the subject will have to touch areas on the side of the display to guide the agent to the left or right of what would be their default trajectory if they touched the screen only in the centre of the arc of virtual fruits (that would not result in receiving rewards). During this stage, subjects will also learn the effects that touching different parts of the screen have (walking forward, walking and turning, turning on the spot, see Fig. 1). In addition, subjects repeatedly experience how real life reward (receiving a piece of real fruit from the experimenter) is associated with on-screen events that correspond to the agent "walking into" specific objects (the virtual fruit).

Finally, in the stage that follows (Stage 3, or "Small Scatter", in Tables 1 and 2), the virtual fruit array surrounding the invisible first-person agent at the beginning of the trial becomes even less structured (see Fig. 5). Many individuals are already able to locate and touch virtual fruit objects by the time they reach this stage (as opposed to other on-screen objects), but many of them are not. For some subjects, their manual precision is still not exact enough to guarantee that the agent walks into the piece of virtual fruit that the subject is aiming for, sending the agent on a path farther and farther away from virtual fruit. To balance giving subjects freedom to explore, and keeping their motivation up, this stage comes with several sub-stages. At the beginning, when the virtual agent loses sight of virtual fruit, or continuously bumps into an obstacle, the experimenter is instructed to wait for four seconds and then intervene by taking over control over the agent (via a keyboard trackpad or mouse attached to the testing computer) and turning the agent on the spot until they see virtual fruit again. Once the subject masters this earliest sub-stage (Stage 3 A, 4 seconds to intervention), they are promoted to the next sub-stage (Stage 3B, 8 seconds to intervention), and so on. This approach of slowly "taking off the training wheels" was designed to ensure that subjects will continue to get rewarded and stay motivated while experiencing the consequences of walking the agent in

Table 2
Overview of individual training steps and pass criteria.

Stage 1: Concentric circles (Fig. 3)	
Aim: Subjects with no prior touchscreen experience must first learn to associate touching the screen with receiving a reward. As the agent begins surrounded by virtual fruit, subjects are very likely to guide the agent into virtual fruit and earn rewards without difficulty.	
Trial set-up	• The agent begins a trial surrounded by three circles of virtual fruit, each of a different type • Virtual fruit circles had radiuses of 4, 8, and 12 m, that also reflect their distances from the avatar's starting location
Procedure	• The trial ends either after 3 virtual fruits are collected ("correct trial"), a time out of 30 seconds (= a total elapsed time of 30 seconds since the start of the trial), or if the experimenter ends the trial • Each session consists of 10 trials
Experimenter assistance	• Initiates trial for subject • Offers verbal encouragement • Encourages subject to touch the screen (e.g., knocking against monitor from the back, calling ape's name, gesturing, etc.) • Ends the trial if the agent wanders away from the circles more than the distance of approximately 3 virtual fruits
Pass criterion	• 10 correct trials (3 virtual fruits collected) across any number of sessions
Stage 2: Concentric circles with a gap (Fig. 4)	
Aim: Now subjects must begin directing their touches to virtual food items in the game. If they are not paying attention to what is on the screen, they are likely to move the agent through the gap in the concentric circles and not collect any virtual fruit.	
Trial set-up	• Agent begins trial surrounded by three circles of virtual fruit with a gap in the start view line of vision. • Set-up is otherwise identical to Stage 1.
Procedure	• As in Stage 1
Experimenter assistance	• As in Stage 1
Pass criterion	• 10 correct trials (3 virtual fruits collected) across any number of sessions
Stage 3: Small scatter (Fig. 5)	
Aim: Subjects must now make the agent travel slightly further to collect virtual fruit, requiring some orienting and a little persistence as virtual fruit will not always be visible on the screen (i.e., it may be behind the agent).	
Trial set-up	• Agent begins surrounded by different types of virtual fruit, slightly further away than in the previous stages. The same layout of targets was used each trial. Euclidian distances between the avatar starting location and virtual fruit items, disregarding small height differences in the terrain, ranged from 2.7 to 8.9 m. • Five of each type of virtual fruit are present (e.g., 5 apples, 5 grapes, and 5 bananas) • *Group setting: 6 virtual fruits (2 of each type)*
Procedure	• Trial ends after all virtual fruit is collected or after a time out of 300 seconds (5 minutes) • Each session consists of 2 trials • *Group setting: 5 shorter trials, 240 second timeout*
Experimenter assistance	• Initiates trial if the subject doesn't do so within 15 seconds • Offers verbal encouragement • Encourages subject to touch the screen • If the subject runs into problems for N seconds, the experimenter will turn the agent and move it back to nearer the virtual fruit: o Problems: ▪ The subject has moved the agent away so that all virtual fruit is out of sight and/or has not touched the screen for N seconds (regardless of whether the agent is resting or continuing to walk) ▪ The agent is stuck at an obstacle and is bouncing off the obstacle or is resting for N seconds • If virtual fruit is visible behind the obstacle, the experimenter will steer them around until the nearest virtual fruit is accessible with no additional bouncing o Number of seconds to wait before experimenter intervention: ▪ Stage 3 A: N = 4 ▪ Stage 3B: N = 8

(*continued on next page*)

Table 2 (*continued*)

Stage 1: Concentric circles (Fig. 3)	
	▪ Stage 3 C: N = 12 ▪ If the subject has left the screen, the experimenter calls them back after the intervention o Proximity to virtual fruit that experimenter should move the agent: ▪ First instance since last fruit collection: approximately 5 seconds walking distance ▪ Second instance since last fruit collection: (if problem occurs again within the same trial, without having collected virtual food in between) approximately 2 seconds walking distance ▪ Third instance (and more): 1 second walking distance
Pass criterion	• To pass each sub-stage (3 A, 3B, 3C), two sessions with two successful trials (= all virtual fruit collected before time out) • To pass Stage 3: a total of four successful trials (across any number of sessions, across any sub-stage) with all virtual fruit collected with no help from the experimenter, other than verbal encouragement • *Group setting with 5 shorter trials:* o *Sub-stages: 10 successful trials (all virtual fruit collected) across any number of sessions, per sub-stage* o *Stage 3: 10 successful trials (all virtual fruit collected) with no help from the experimenter, across any number of sessions, across any sub-stage*
Stage 4: Medium scatter (Fig. 6)	
Aim: Subjects will have to make the agent travel even further between virtual food items, requiring orienting, obstacle avoidance, and some persistence when virtual fruit is not visible.	
Trial set-up	• Virtual fruit is randomly dispersed in the central area of the arena. The same randomized layout of targets is used in each trial. Euclidian distances between the avatar starting location and virtual fruit items, disregarding small height differences in the terrain, ranged from 6.4 to 26.4 m • Five of each type of virtual fruit are present (e.g., 5 apples, 5 grapes, and 5 bananas)
Procedure	• Trial ends after all virtual fruit is collected or after a time out of 300 seconds (5 minutes) • Each session consists of 2 trials
Experimenter assistance	• No more assistance other than verbal encouragement
Pass criterion	• Two sessions in which all virtual fruit is collected in both trials, with no help • *Alternative: 8 trials with at least 8 of the available 15 virtual fruits collected*
Stage 5: Large scatter (Fig. 7)	
Aim: Subjects will have to make the agent travel further again between virtual food items, travelling around the entire arena. This requires more orienting, more obstacle avoidance, and more persistence when virtual fruit is not visible.	
Trial set-up	• Virtual fruit is randomly dispersed all around the arena. The same randomized layout of targets is used in each trial. Euclidian distances between the avatar starting location and virtual fruit items, disregarding small height differences in the terrain, ranged from 16.5 to 43.6 m. • Five of each type of virtual fruit are present (e.g., 5 apples, 5 grapes, and 5 bananas)
Procedure	• As in Stage 4
Experimenter assistance	• As in Stage 4
Pass criterion	• As in Stage 4

different directions and into different objects. Because of the COVID-19 pandemic, testing the orang-utans was interrupted before they had completed all five stages of the training procedure. Testing resumed in June 2023 with 3 of the original orang-utans and 1 new orang-utan.

2.3.1.2. Subjects in a group setting: adjusting experimental flow and training criteria. Although two chimpanzees in Edinburgh (4-year-old and 25-year-old males, Velu and Frek) made good progress with the less structured approach that we took with the original touchscreen-experienced Leipzig group of chimpanzees, other members of the social group were making slower progress. Once we had developed the more structured approach with the orang-utans (outlined above), we implemented this with the Edinburgh group of chimpanzees, tailoring each subject's starting stage to their current performance.

Starting out with this more consistent, small-steps training procedure, we saw continuous improvement in the Edinburgh chimpanzees' mastery of the VE navigation. However, a new challenge to the experimenters that came with the group setting, was the less structured and less predictable nature of data collection. When testing subjects individually in Leipzig, all subjects would usually complete their scheduled testing session in one sitting, and there was time in between subjects for the experimenter to re-set the program as needed (such as entering the subject's name and selecting their session procedure scheduled for that day). In the Edinburgh group-setting testing, subjects may approach and leave the screen numerous times throughout a session, sometimes leaving mid-trial, and so the experimenter often needed to switch from one individual's daily scheduled session quickly to another's. For this reason, we added a function to APExplorer that allowed for immediate switching between subjects using keyboard inputs (for more information, see Schweller et al., 2022). For example, Subject A might participate for half of trial 1 and leave, Subject B might then complete 2 trials, and then Subject A might return and resume exactly where they left off in trial 1 with all relevant parameters being exactly what they were when the subject left (time left in trial, virtual fruit remaining, agent location and bearing).

The group testing situation in Edinburgh also motivated us to track progress in smaller bouts than in Leipzig. In Leipzig, subjects are tested individually for a session that allows completing all scheduled trials over a period of 10–20 minutes, on most days and for most subjects. In Edinburgh, a subject may, for example, participate for 2 minutes, leave, then return for another 2 minutes, and so on, and may contribute less than 10 minutes' worth of testing time on a given day. This has implications for how much virtual fruit they will direct the agent to collide with on a given day, regardless of their level of mastery of the touchscreen input mechanics. For example, we noticed quickly that the criterion we had adapted from training orang-utans in Leipzig for promoting subjects from sub-stage to sub-stage of Stage 3, that was passing 4 trials by collecting all 15 virtual fruits (see Table 2), would often leave subjects in Edinburgh stuck on a sub-stage. We considered that this lack of progression may in some cases have resulted from chimpanzees not participating for long enough to collect all 15 pieces across multiple short bursts of interacting with the touchscreen, and not necessarily from being too inefficient at collecting virtual fruit. Therefore, we adjusted Stage 3 for the Edinburgh chimpanzees by presenting (and requiring passing) more trials, but with a smaller number of virtual fruits per trial.

After developing this training protocol to overcome the challenges described above, we implemented the version of the training used with the Leipzig orang-utans with a new group of chimpanzees at Leipzig Zoo. Below, we outline the training procedure and the training progress with three groups: the new group of Leipzig-housed chimpanzees, Leipzig-housed orang-utans, and the Edinburgh-housed chimpanzees.

2.3.2. Training procedure

The main gameplay mechanisms we required subjects to master before moving on to experiments with the VEs were twofold:

– Learning to move the agent (walk forwards and turn on the spot)
– Learning to identify and collect virtual fruit (both close to their current location and further in the distance)

Thus, our training focused on subjects learning to collect virtual food and navigate a space occupied by various obstacles with no assistance, reflected in our pass criteria. Once all training stages were completed and passed, we considered subjects ready to move on to participate in experiments within VEs. A brief overview of the training stages is given

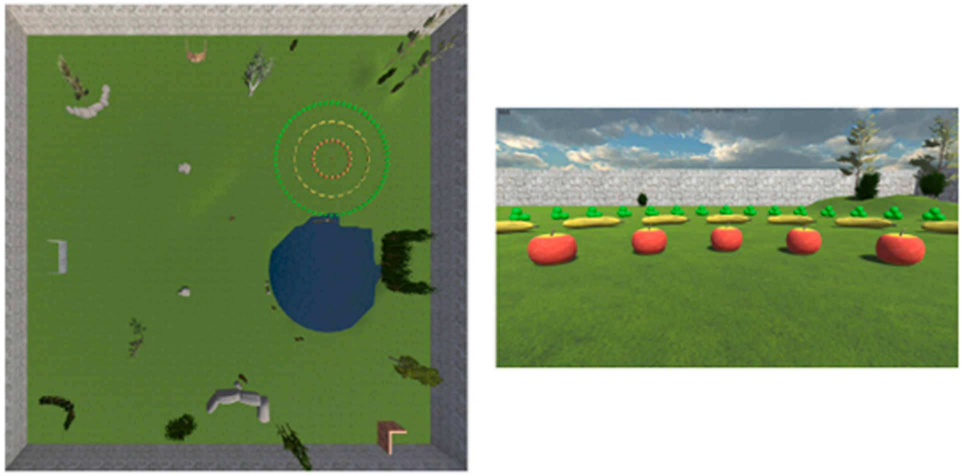

Fig. 3. Birds-eye view (left) and agent start view when monitor aspect ratio is 16:9 (right) of Stage 1 (concentric circles).

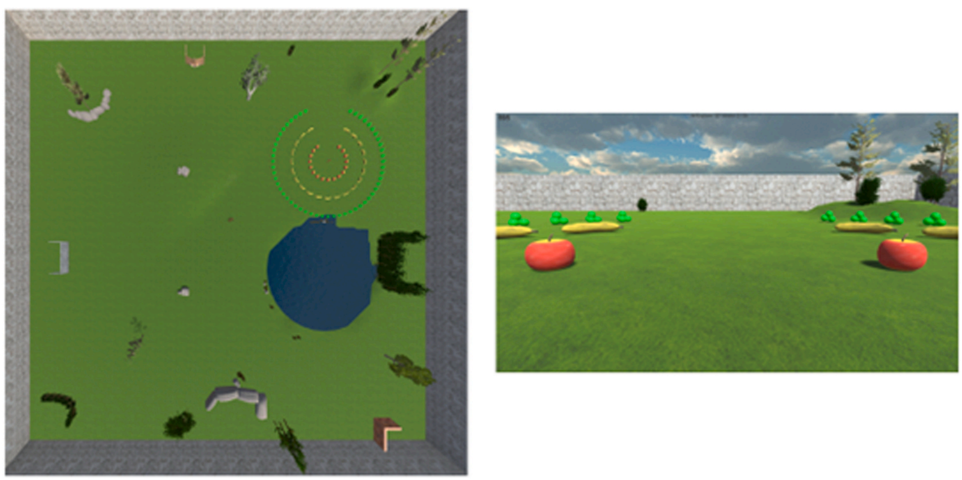

Fig. 4. Birds-eye view (left) and agent start view when monitor aspect ratio is 16:9 (right) of Stage 2 (concentric circles with a gap).

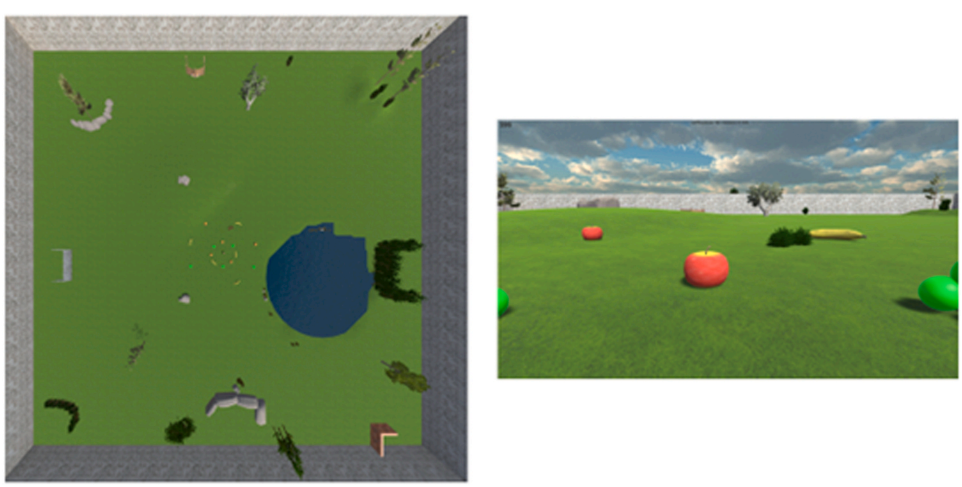

Fig. 5. Birds-eye view (left) and agent start view when monitor aspect ratio is 16:9 (right) of Stage 3 (small scatter).

in Table 1, and a more detailed outline can be found in Table 2. It should be noted that although rules were in place for the experimenter regarding when and how to intervene, these were not always strictly adhered to, and we aimed to provide a general guideline while maintaining some flexibility. The detailed outline provided in Table 2 reflects our recommendations for training. We note that this protocol was under development while training the groups of apes included here, and some aspects of the protocol were modified between groups. Details

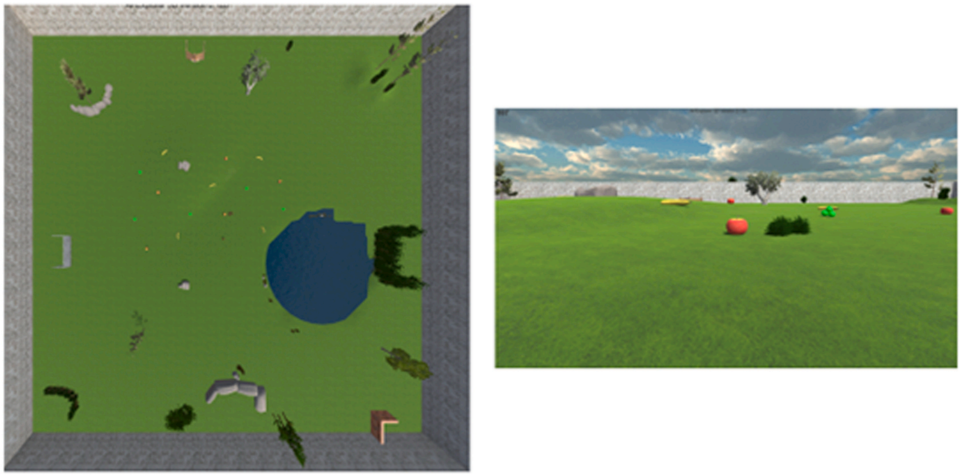

Fig. 6. Birds-eye view (left) and agent start view when monitor aspect ratio is 16:9 (right) of Stage 4 (medium scatter). Image is a modified version of an image from Allritz et al., (2022), supplementary materials, reprinted here with permission from the image's creators (ESM, MA).

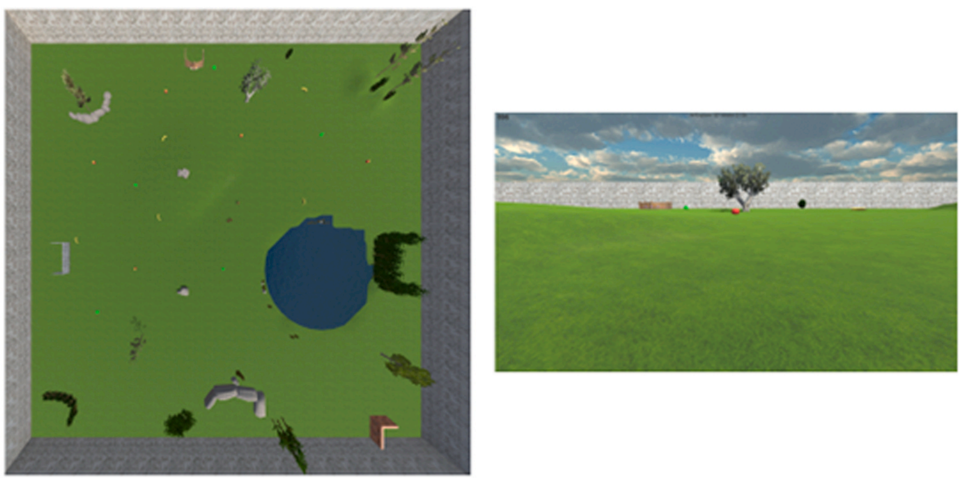

Fig. 7. Birds-eye view (left) and agent start view when monitor aspect ratio is 16:9 (right) of Stage 5 (large scatter). Image is a modified version of an image from Allritz et al., (2022), supplementary materials, reprinted here with permission from the image's creators (ESM, MA).

of how subjects in each group deviated from the protocol in Table 2 are described in the results sections.

3. Results

Here, we provide an overview of the time taken, in number of trials and testing days, for three groups of subjects to complete the training outlined above. The number of trials includes all trials attempted by subjects, both complete and incomplete. A "testing day" is a day on which the task was made available to a subject, and, in addition, they attempted the training/touched the screen in at least one trial.

The training protocol above was developed throughout training these subjects and was not always followed exactly this way for all subjects reported here. Rather, this is an overview of how long these subjects took with roughly the above protocol, that could inform the approximate length of training of future subjects. We have categorised the stages listed above into the following levels for reporting the time taken to complete training:

- Level 1: Stages 1–2
  - o Subjects are always surrounded by concentric circles of virtual fruit
- Level 2: Stage 3
  - o Virtual fruit with a low degree of scatter, with different times to intervention
- Level 3: Stages 4–5
  - o Virtual fruit with medium and large degrees of scatter

Note that trials in different levels have different maximum durations to account for differences in distances between virtual fruit items and the amount of experimenter help between levels (Level 1 [Stages 1 & 2]: 30 seconds, this varied during the development of the training protocol, between 30 and 600 seconds; Level 2 [Stage 3]: 300 seconds, or 240 seconds for the group setting version with 5 shorter trials; Level 3 [Stages 4 & 5]: 300 seconds in later versions, 600 seconds in earlier versions of the training program). This means that in early levels, subjects will also receive more trials per day (see Table 2). To account for this difference, the final columns in Tables 3, 4, and 5 list the total number of testing days a subject required from starting their training to completing the final stage. The supplementary video shows examples of individuals from different groups participating in trials from all five stages. Figure S2 shows the relationship between the age of subjects on their first day of training and the number of trials to criterion.

3.1. Group 1: Leipzig chimpanzees

In the tables below, we present the number of trials each subject completed in total on each of the three levels. Table 3 shows data for the five Leipzig chimpanzees (see also Figs. 8 and 9), four of whom already had some touchscreen experience (everyone but male Azibo).

Discrepancies from training protocol:

- Level 1: 6 trials instead of 10, with a pass criterion of 5/6 correct trials (3 virtual fruits collected).
- Additional sub-stage "3D: small scatter, 24 seconds to intervention" for all subjects but Tai (pass criterion as in above sub-stages). For later versions of the training program, we decided that this stage was not needed as subjects were able to move to Stage 4 after less time with Stage 3.
- For our pass criterion for Stage 3 (four trials without experimenter intervention), we initially had an additional sub-stage "Stage 3E: no intervention". For later versions of the training, as we noticed that subjects often completed trials without assistance earlier in the training process, we decided that trials in which subjects do not need help from the experimenter could occur at any stage and count towards this pass criterion. Level 3 in the tables below include all trials completed by subjects, with and without experimenter assistance.

As detailed in Table 3, the five Leipzig chimpanzees, four of whom already had touchscreen experience, all completed their training within 16–31 days of training (median = 28 days), with daily training sessions of about 10–20 minutes.

One subject, Tai, initially responded with apprehensive, mildly anxious behaviour to the 3D motion and/or the sound cues of the VE (for example, retreating from screen, longer pauses between approaching and touching screen, touching screen while sitting farther away than usual). To address this, we created a version of the first training stage for her without sound, and in which the walking speed was much slower. After 3 sessions with the slower version (included in Table 3 under Level 1), Tai returned to the regular speed version with sound and no longer showed any signs of distress. Robert and Riet also began with this stage, based on the assumption that they may also benefit from "starting slowly"; Robert did 4 sessions and Riet 5 sessions, also included in Level 1 in Table 3.

Tai had by far the most touchscreen experience amongst these chimpanzees and moved to Level 3 after only 2 sessions of Level 2 (without reaching the pass criterion) due to the experimenters deeming her ready. Tai was particularly fast and finished all her training in 16 days, whereas others finished training across 28–31 testing days.

3.2. Group 2: Leipzig orang-utans (no touchscreen experience)

Table 4 presents training data for the Leipzig orang-utans (see also Figs. 8 and 9). All orang-utans had experience with cognitive testing, but none had experience with touchscreen tests when the training began.

Table 3
Number of trials for each level and testing days overall to criterion for Leipzig chimpanzees. The last two columns show the totals for each individual (trials and days) and the bottom row shows the group median of total trials and days. All subjects other than Azibo had prior touchscreen experience.

Subject	Complete	Level 1 (No. Trials)	Level 2 (No. Trials)	Level 3 (No. Trials)	Total (No. Trials)	Total (No. Days)
Tai	yes	49	15	19	83	16
Riet	yes	38	62	12	112	28
Azibo	yes	65	60	13	138	29
Robert	yes	84	56	12	152	28
Daza	yes	96	53	16	165	31
MEDIAN	–	–	–	–	*138*	*28*

Training was conducted over two time periods (see above and Figure S1), the first running from October 2019 to March 2020, and the second running from June to August 2023.

Discrepancies from training protocol:

- Level 1: 6 trials per session instead of 10, with a pass criterion of 5/6 correct trials (3 virtual fruits collected).
- Additional sub-stage "3E: no intervention" (see above).

Two individuals dropped out after the first training period, one (male Suaq) because he left Leipzig Zoo before training resumed, and one (female Raja) because her motivation to participate was lower compared to other orang-utans. Even in initial stages with frequent, easily obtained rewards, Raja would repeatedly participate only for a few trials and then stop engaging with the touchscreen. Three subjects who participated in the first period (females Pini, Dokana, and Padana) also participated in the second. Female Sari participated only in the second period of training. After the break from training (of over 3 years), all subjects moved back to the beginning of the training level before the one they left off on (see details in supplementary Table S2). All individuals that entered the second period had, by that time, gained initial or additional touchscreen training with a 2D task with static images. As can be seen in Table 4, across the four Leipzig orang-utans who completed their training, they did so within 16–37 days of training (median = 26 days), with daily training sessions of about 10–20 minutes, as with the Leipzig-housed chimpanzees. One subject (female Sari) was particularly fast and finished her training within 16 days, that is, in the same amount of time as the fastest and most touchscreen-experienced of the Leipzig chimpanzees did.

Some subjects deviated from the training protocol due to experimenter error, either receiving too few or too many sessions of a training stage (see supplementary materials for details). All sessions are included in Table 4 to provide an accurate account of how many trials of each level subjects completed.

3.3. Group 3: Edinburgh chimpanzees (group setting)

Table 5 shows the training data for the chimpanzees housed in Edinburgh Zoo (see also Figs. 8 and 9). Before moving to the training protocol above, we administered a combination of Level 2 and Level 3 stages to some subjects to evaluate how they performed, which subsequently helped us to design the incremental training programme. This is referred to in Table 5 as 'pre-training exposure'. For some subjects who completed this pre-training exposure, they subsequently skipped Level 1 and moved straight to Level 2. The total number of test days includes the pre-training. The median number of test days only includes those subjects who completed the training.

Discrepancies from protocol:

- Level 1 includes a piloted but later removed stage similar to concentric circles but with only 3 virtual fruits in front of the agent, with a pass criterion of collecting all 3 of these virtual fruits. We added trials in which the agent is surrounded by virtual fruit circles (in Stage 1: concentric circles), considering that these may increase reward frequency (and hence, motivation to participate), as running into virtual food is not dependent on the agent's heading direction at the start of the trial. That is, the subject can touch the screen to direct the agent in any direction and the agent will eventually collide with virtual food.
- Additional sub-stage "3D: 24 seconds to intervention" (see above).
- Additional sub-stage "3E: no intervention" (see above).

As can be seen in Table 5, Edinburgh chimpanzees took longer than Leipzig apes on average, in terms of total number of testing days, to pass all levels of the VE training. Of the 15 chimpanzees who participated, 11 had finished their training within between 37 and 156 testing days

Table 4
Number of trials for each level and testing days overall to criterion for Leipzig orang-utans. The last two columns show the totals for each individual (trials and days) and the bottom row shows the group median of total trials and days. The central white column labelled 'break' indicates the long testing break discussed in text, with columns to the left indicating participation prior to the break and columns to the right indicating the time after the testing break. Asterisks indicate stages not yet completed, and the total counts that are not included in the medians. Dashes in a cell indicate that the subject was not presented with that training stage. Totals include trials and days both before and after the testing break. Medians only include those subjects that completed training.

Subject	Complete	Level 1 (No. Trials)	Level 2 (No. Trials)	Level 3 (No. Trials)		Level 1 (No. Trials)	Level 2 (No. Trials)	Level 3 (No. Trials)	Total (No. Trials)	Total (No. Days)
Pini	yes	12	16	14	***BREAK (>3 years)***	–	8	8	58	26
Dokana	yes	12	17	14		–	8	12	63	29
Padana	yes	36	23	–		30	14	14	117	37
Sari	yes	–	–	–		24	12	12	48	16
Raja	no	42 *	–	–		–	–	–	42 *	12 *
Suaq	no	36	14 *	–		–	–	–	50 *	14 *
MEDIAN	–	–	–	–		–	–	–	*61*	*26*

Table 5
Number of trials and testing days to criterion for Edinburgh chimpanzees. The last two columns show the totals for each individual (trials and days) and the bottom row shows the group median of total trials and days, including only those individuals who have passed all training stages. Asterisks indicate stages not yet completed, and the total counts that are not included in the median. Dashes in a cell indicate that the subject was not presented with that training stage.

Subject	Complete	Pre-training exposure (No. Trials)	Level 1 (No. Trials)	Level 2 (No. Trials)	Level 3 (No. Trials)	Total (No. Trials)	Total (No. Days)
Velu	yes	2	–	3	40	45	37
Frek	yes	18	–	13	26	57	39
Louis	yes	–	–	84	21	105	54
David	yes	1	–	86	28	115	63
Liberius	yes	8	–	136	31	175	110
Kilimi	yes	13	63	81	30	187	85
Qafzeh	yes	15	78	79	22	194	81
Masindi	yes	–	100	96	16	212	82
Edith	yes	8	68	118	34	228	110
Eva	yes	5	127	99	17	248	66
Lucy	yes	5	436	99	32	572	156
Heleen	no	–	11 *	–	–	11 *	5 *
Paul	no	2	73	39 *	–	114 *	35 *
Sophie	no	5	104	8 *	–	117 *	44 *
Rene	no	2	97	72 *	–	171 *	62 *
MEDIAN	–	–	–	–	–	*187*	*81*

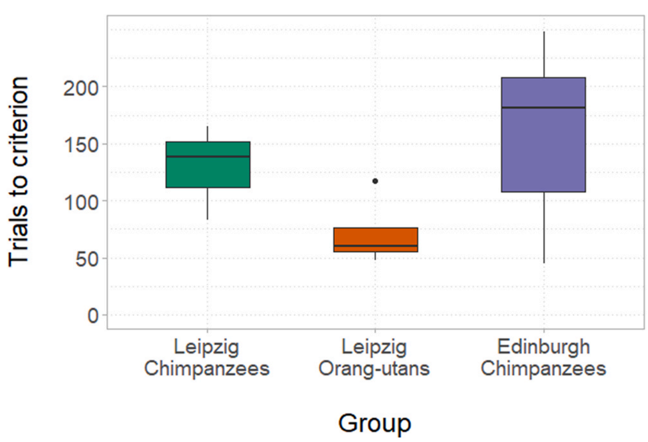

Fig. 8. Number of trials to pass all training stages across groups (including only those subjects who have completed all training stages). The central line of the boxplot shows the median, the coloured boxes show the IQR, and the whiskers indicate the minimum and maximum values of the data within 1.5 x IQR. Data outside of this range are plotted as separate outlying points. One outlying data point was omitted from this figure for clarity (Edinburgh chimpanzee Lucy, 572 trials).

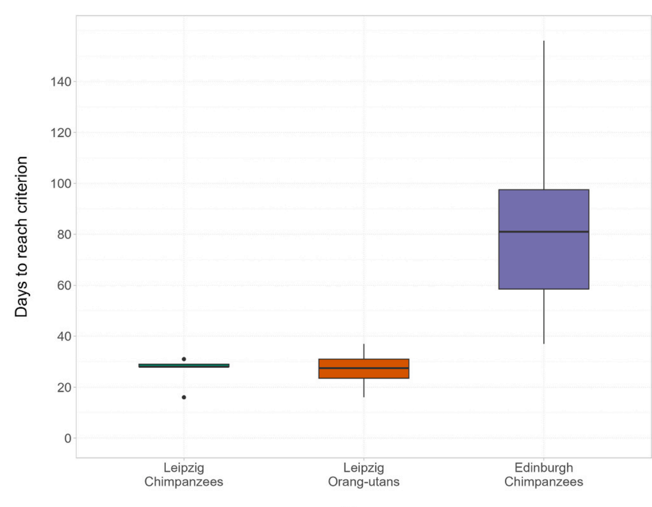

Fig. 9. Number of days to pass all training stages across groups (including only those subjects who have completed all training stages). The central line of the boxplot shows the median, the coloured boxes show the IQR, and the whiskers indicate the minimum and maximum values of the data within 1.5 x IQR. Data outside of this range are plotted as separate outlying points.

(median = 81 days), in part reflecting the less consistent data collection routine described above. Four individuals had not completed their training at the time of preparing this article. With regard to estimating the necessary time investment when applying this protocol at other sites, it is also important to note that the number of training days reported is not identical to the number of days on which we made the training task available; some individuals participate almost every day that touchscreen testing is offered, whereas others participate more sporadically. Individual differences in the overall time spent training will thus result from a mixture of actual learning speed, frequency of participation, and duration of participation.

4. General discussion

Virtual environments present a vast range of opportunities to study old and new questions in animal cognition in novel ways. Building upon the freely available 3D virtual environment software "APExplorer_3D" (Schweller et al., 2022), our goal in this article was to present a training method that allows nonhuman primates with different training needs to learn quickly to participate in a range of virtual environment tasks. We have conveyed the principles of our training method to other researchers in a way that we hope makes it easy to reproduce and modify it according to their needs, either with APExplorer_3D or with comparable, custom-made software.

Across three training periods, we presented three different populations of zoo-housed great apes with a training system designed to teach subjects the basic gameplay mechanics of touchscreen-guided navigation in virtual 3D environments. By the end of training, great apes could initiate trials and operate the touchscreen without human assistance; differentiate virtual food from virtual non-food objects; and navigate towards virtual food by approaching already visible items, by avoiding obstacles, and by rotating the virtual agent in search for virtual food when none was visible. By the end of Level 3, subjects could touch a touchscreen in different positions to bring an invisible avatar (first-person perspective) into contact with each of 8–15 targets that were widely scattered over a simulated surface area of 100 m squared, and they could do so in under a 5-minute time limit. Built around a philosophy of gradually increasing the challenge set before the individual, while avoiding frustration or long stretches without rewards, our method allowed almost all subjects to complete all training steps over the course of only a few months.

Regarding median training times in our relatively small groups of apes (28 days for Leipzig-housed chimpanzees, 26 days for Leipzig-housed orang-utans, and 81 days for Edinburgh-housed chimpanzees), the difference that stands out the most is the one between apes in Leipzig and those in Edinburgh. Only two of the Edinburgh chimpanzees (males Frek and Velu) passed training after less than 40 testing days, and thus in an amount of time comparable to Leipzig chimpanzees and orang-utans, whereas all other Edinburgh chimpanzees took longer (54 testing days and more). This could in part be a consequence of the different testing situations at both sites – with Edinburgh apes being more frequently interrupted or distracted while testing, and, on average, time spent testing per day being shorter in Edinburgh. This difference notwithstanding, variation in how subjects were selected by the experimenters for participation and continuation at the two sites may have contributed to the difference in median training times (for example, Leipzig chimpanzees: selection of apes with lots of testing room experience and, in many cases, touchscreen experience; Edinburgh chimpanzees: zero prior selection). Related to this, differences in the total number of individuals that ended up participating at both sites may further have contributed to observing a wider range of training days to criterion across subjects in Edinburgh. Considering only the apes tested in Leipzig, training times were numerically quite similar between the five mostly touchscreen-experienced chimpanzees (16–31 days) and the three, at least initially, touchscreen naive orangutans who completed VE training (26–37 days). We hope that this relatively speedy acquisition of the basic VE input mechanics by the subjects will encourage other researchers to adopt these methods.

Our training system was intended to address two major challenges that researchers may face when attempting to train new groups of primates for virtual environment studies. The first potential challenge is to train subjects who have little to no touchscreen experience. Here, we trained a group of orang-utans, the majority of whom had little or no prior experience with touchscreen tests when they started their VE training. In order for subjects to be able to learn about the game mechanics from on-screen feedback and from behaviour-reward contingencies, subjects must be encouraged to interact with the screen in the first place. To encourage frequent touching from the beginning, our training method used a number of different approaches: subjects are encouraged verbally and with gestures made by the experimenter to touch the screen, and trials are set up so that even touching the screen only once or twice will result in immediate rewards from very early on. As subjects become comfortable with approaching and touching the screen, experimenter encouragement is slowly faded out, and the individual's challenge – the number of touches required, the time passing between reward collections, etc. – is gradually increased, in line with the subject's current state of competency. In our training of the Leipzig orang-utans, despite the relative complexity of the stimuli, 4 of 5 subjects interacted with the touchscreen from the first sessions, and progressed quickly and steadily through the training stages, moving through multiple training stages in a matter of weeks. Keeping the training protocol flexible and adaptable allowed subjects to receive help from the experimenter as and when they needed it during early trials.

A second challenge that researchers at many sites will face is that subjects cannot be tested individually and are instead tested in a group setting. All Edinburgh chimpanzees participated in a group setting. Although beneficial for group cohesion and social learning, group testing may introduce many opportunities for training disruptions, including distractions from noise and third-party interactions, invitations from other subjects for social interactions, or displacement from the touchscreen by more dominant individuals. This means that participation may be sporadic or fragmentary and subjects may leave or be interrupted mid-trial. Our training system addressed this by allowing fast switching between subjects, which allowed subjects to always pick up exactly where they had left off. In addition, we eventually adapted our training protocol to match the needs of those subjects who were participating for less than a full session on most days. Tracking cumulative performance across consecutive testing days, even when only a few virtual fruits were collected on each day, allowed us to detect progress and gradually promote every subject according to their level of skill in this group setting.

Our training method was designed to achieve specific, successive milestones related to simple 3D environment "foraging", including being able to efficiently approach visible items, to differentiate virtual food from virtual non-food items, and to persevere and to search by rotating when no virtual food is visible. The results presented here suggest that this method can be applied to a number of primate groups tested under different conditions. But the method is not without limitations, and how other species will achieve these milestones will most likely differ from site to site. Researchers who have worked with their study species for years will know best whether to introduce additional or alternative training steps, and we encourage them to do so if necessary. For example, if some subjects are keen to participate but do not touch the screen at first, additional, even simpler training steps may be added at the beginning of training. This may include, for example, allowing individuals to observe others who already use the touchscreen. Another method we have used, but for which we only have anecdotal, rather than systematic empirical evidence of success, is initial training without a touchscreen that involves interaction with the experimenter. The experimenter indicates a location at the window or mesh that separates them from the subject, and which is adjacent to the touchscreen (by pointing or by holding up food), and the subject gets rewarded for touching the corresponding location on their side of the window. This is repeated until the subject's hand "follows" the experimenter's reliably until the experimenter eventually moves their hand to a location behind the touchscreen, encouraging the subject to touch the corresponding location on their side. Further, once the subject does touch the screen, early trials of Stage 1 training may also be set up in a way that requires even less touching, for example, by placing virtual food items even more narrowly around the agent. Similarly, if subjects only touch the screen centre at first, more intermediate steps could be introduced to Stage 2 in which the gap in the three concentric circles increases more gradually across sessions – this has already proved successful in the training of additional chimpanzees at Leipzig Zoo not reported in this article. Analogously, if in the Stage 3 sub-stages the increasing perseverance requirements are too abrupt for some subjects, different parameters can be more gradually adjusted to recalibrate the level of challenge, for example, the time to intervention, the speed of the agent, or the distance to the virtual food. These additional sub-stages are all easily added within the APExplorer software (Schweller et al., 2022).

A factor that currently limits strict methodological reproducibility of our method is that Stages 3A-3C require the experimenter to manually intervene and take over control of the agent when pieces of virtual fruit are outside the agent's view for specified periods of time. As detailed above, these elements were added to the protocol to strike a balance between providing the subject with time for self-guided learning on the one hand, and avoiding extended periods without reward, and thus, frustration, on the other hand. Although the protocol is clear about the amount of time after which the experimenter should intervene, and an on-screen timer helps the experimenter keep track of time passed, lapses in the experimenter's attention, or spontaneous, subjective decisions on when and where exactly to click may introduce bias such that, for example, different experimenters may train individuals in slightly different ways. Whilst our training system is meant to be adaptive and very strict reproducibility of the method was not one of our major concerns, where strict reproducibility or full automation is desired, future applications of the training protocol could automate these kinds of intervention.

A challenge that our training method addresses only partially is the level of distraction and the potential for displacement for subjects tested in group settings. This can be addressed in a number of ways that are not straightforward to implement but that may be worth the additional effort. For example, many sites that test subjects in groups set up multiple touchscreen stations, sometimes with physical partitions, to minimize displacement and distraction (for example, PRI / E-Hub: Martin et al. 2014, CNRS primate facility: Fagot and Paleressompoulle 2009, Heidelberg Zoo: Schmitt, 2019). At some sites, a keeper or a second experimenter distracts individuals while they wait their turn, and some sites use subject-unique "end screens" to signal to individuals that they, specifically, have completed their training for the day (Leinwand et al., 2020; Martin et al., 2022).

The methods outlined in this article were aimed to train subjects on the basic gameplay mechanisms we believed were most important to master before moving on to participating in virtual environment experiments. Although subjects may understand how to move an agent around the virtual space to maximize reward, we cannot make rich inferences about how they represent this space at this point. A recent study by Koopman et al. (in press) demonstrated that chimpanzees navigating virtual environments were able to guide the agent towards previously seen but now out-of-sight virtual rewards in efficient ways, ruling out at least the very simplest of associative learning accounts of moving the agent to contact virtual fruit. Nonetheless, it will require many further experiments to convincingly establish whether virtual environments can be experienced as a three-dimensional space or whether lower-level associative mechanisms are used by subjects to move the agent through the environment. Indeed, perceptual differences have been found between humans and chimpanzees when viewing two-dimensional stimuli casting shadows to give an illusion of three-dimensionality (Tomonaga and Imura, 2010), whereas similarities have been found between the two species in their sensitivity to concave shape deformation, a feature related to the perception of three-dimensionality (Matsuno and Tomonaga, 2007). The acquisition of the ability to move through the environment is the first step towards running experiments with VEs, some of which could investigate the spatial cognition employed to navigate them and elucidate how VEs are perceived by primates.

We were impressed with the speed of acquisition in some individuals at all sites. Yet, the extent to which the behaviours we trained in our navigation training, and the cognition underlying them, generalize to enable other problem-solving strategies related to spatial cognition in VEs (for example, object permanence, shortcutting, detouring, spatial memory, etc.) remains a matter for empirical investigation, and it may in many cases require additional training steps that encourage such generalization. VEs will allow for new levels of creative experimental design, not only in spatial cognition but also in social cognition and other domains. However, our development of optimal, tailored training methods that allow primates to apply their cognitive abilities to problems in virtual space is still in its infancy.

Regarding the use of touchscreens in our training method, one anonymous reviewer pointed out that this may not yet be the best input method for investigating how nonhuman primates navigate virtual space. Arguably, joysticks, as they have been used for VE navigation by great apes in a previous study (Dolins et al., 2014), may have certain advantages, advantages that similarly apply to trackballs as input devices (Kaneko and Tomonaga, 2011, 2012). One potential advantage is that joysticks confer more fine-grained control to the subject, as the agent walks only when the joystick is actively manipulated (rather than indefinitely to a touched location in the touchscreen version). Requiring more fine-grained control may also be achieved when touchscreens serve as input device, for example, when input mechanics are changed so that agents will only walk a certain distance when the screen is touched, and multiple touches are required for moving farther. More importantly, when joysticks serve as input devices, the subject always has a full view of the monitor, as the monitor does not need to be touched (and thereby covered) by the subject. Future studies should directly compare different input methods to compare benefits and disadvantages regarding different dimensions, for example, ease of training, evidence of perceiving the task as truly three-dimensional, and others.

We have presented here a flexible yet structured method of training non-human apes to use virtual environments via touchscreen input. The method can be used with subjects without any prior touchscreen experience and can be implemented in group settings, making it suitable for many sites, and not limited to research settings in which animals can be tested individually or have extensive testing experience. We hope that these methods can be used by other researchers to run VE experiments with numerous subjects and species. Indeed, during the preparation of this article this training method has since been implemented (and in many cases completed) with additional chimpanzees (across Leipzig Zoo and ARTIS Zoo), touchscreen-naïve bonobos (across Leipzig Zoo and Twycross Zoo), touchscreen-experienced gorillas (Leipzig Zoo), and capuchin monkeys with and without touchscreen experience (Edinburgh Zoo). VEs will make possible novel kinds of experiments in captive settings for studying animal cognition in domains like spatial learning and navigation, cooperation and competition, and others. In addition, assessing the cognitive enrichment value and potential, and the intrinsic motivation to explore VEs would be another interesting application of this software. Thus, although we have focused on extending the use of this software to other research settings, the software and training method may also be of interest to those interested in exploring digital enrichment with animals, such as animal care staff.

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CRediT authorship contribution statement

Emma Suvi McEwen: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Matthias**

Allritz: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Josep Call:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Sarah E. Koopman:** Writing – review & editing, Investigation, Data curation. **Emilie Rapport Munro:** Writing – review & editing, Investigation, Data curation. **Cristóbal J. Bottero Cantuarias:** Writing – review & editing, Investigation, Data curation. **Charles R. Menzel:** Writing – review & editing, Software, Methodology, Funding acquisition, Conceptualization. **Francine L. Dolins:** Writing – review & editing, Software, Methodology, Funding acquisition, Conceptualization. **Karline R.L. Janmaat:** Writing – review & editing, Software, Methodology, Funding acquisition, Conceptualization. **Kenneth Schweller:** Writing – review & editing, Visualization, Software, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2024.105126.

Data availability

The files required to run the protocol described in this paper, as well as the training data, can be found in the following OSF repository: https://osf.io/wqzj3/?view_only=735ebc1bb6dd4255963743ded64e922e. A free version of the software can be downloaded at osf.io/sx5pm (Schweller et al., 2022).

References

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

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

Allritz, M., Call, J., Schweller, K., McEwen, E.S., de Guinea, M., Janmaat, K.R.L., Menzel, C.R., Dolins, F.L., 2022. Chimpanzees (*Pan troglodytes*) navigate to find hidden fruit in a virtual environment. Sci. Adv. 8 (25), eabm4754. https://doi.org/10.1126/sciadv.abm4754.

Altschul, D.M., Wallace, E.K., Sonnweber, R., Tomonaga, M., Weiss, A., 2017. Chimpanzee intellect: Personality, performance and motivation with touchscreen tasks. R. Soc. Open Sci. 4 (5), 170169. https://doi.org/10.1098/rsos.170169.

Beran, M.J., Pate, J.L., Washburn, D.A., Rumbaugh, D.M., 2004. Sequential responding and planning in chimpanzees (*Pan troglodytes*) and Rhesus Macaques (*Macaca mulatta*). J. Exp. Psychol.: Anim. Behav. Process. 30 (3), 203–212. https://doi.org/10.1037/0097-7403.30.3.203.

Corrigan, B.W., Gulli, R.A., Doucet, G., Martinez-Trujillo, J.C., 2017. Characterizing eye movement behaviors and kinematics of non-human primates during virtual navigation tasks. J. Vis. 17 (12), 15. https://doi.org/10.1167/17.12.15.

Dolins, F.L., Klimowicz, C., Kelley, J., Menzel, C.R., 2014. Using virtual reality to investigate comparative spatial cognitive abilities in chimpanzees and humans. Am. J. Primatol. 76 (5), 496–513. https://doi.org/10.1002/ajp.22252.

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

Dombeck, D.A., Reiser, M.B., 2012. Real neuroscience in virtual worlds. Curr. Opin. Neurobiol. 22 (1), 3–10. https://doi.org/10.1016/j.conb.2011.10.015.

Evans, T.A., Beran, M.J., Chan, B., Klein, E.D., Menzel, C.R., 2008. An efficient computerized testing method for the capuchin monkey (*Cebus apella*): Adaptation of the LRC-CTS to a socially housed nonhuman primate species. Behav. Res. Methods 40 (2), 590–596. https://doi.org/10.3758/BRM.40.2.590.

Fagot, J., Paleressompoulle, D., 2009. Automatic testing of cognitive performance in baboons maintained in social groups. Behav. Res. Methods 41 (2), 396–404. https://doi.org/10.3758/BRM.41.2.396.

Gao, J., Su, Y., Tomonaga, M., Matsuzawa, T., 2018. Learning the rules of the rock–paper–scissors game: Chimpanzees versus children. Primates 59 (1), 7–17. https://doi.org/10.1007/s10329-017-0620-0.

Harvey, C.D., Collman, F., Dombeck, D.A., Tank, D.W., 2009. Intracellular dynamics of hippocampal place cells during virtual navigation. Nature 461 (7266), 941–946. https://doi.org/10.1038/nature08499.

Herrelko, E.S., 2011. An assessment of the development of a cognitive research programme and introductions in zoo-housed chimpanzees. University of Stirling, Stirling, UK. ⟨http://dspace.stir.ac.uk/handle/1893/3654⟩.

Herrelko, E.S., Vick, S.J., Buchanan-Smith, H.M., 2012. Cognitive research in zoo-housed chimpanzees: Influence of personality and impact on welfare. Am. J. Primatol. 74 (9), 828–840. https://doi.org/10.1002/ajp.22036.

Hori, E., Nishio, Y., Kazui, K., Umeno, K., Tabuchi, E., Sasaki, K., Endo, S., Ono, T., Nishijo, H., 2005. Place-related neural responses in the monkey hippocampal formation in a virtual space. Hippocampus 15 (8), 991–996. https://doi.org/10.1002/hipo.20108.

Kaneko, T., Tomonaga, M., 2011. The perception of self-agency in chimpanzees (*Pan troglodytes*). Proc. Biol. Sci. 278 (1725), 3694–3702. https://doi.org/10.1098/rspb.2011.0611.

Kaneko, T., Tomonaga, M., 2012. Relative contributions of goal representation and kinematic information to self-monitoring by chimpanzees and humans. Cognition 125 (2), 168–178. https://doi.org/10.1016/j.cognition.2012.07.006.

Kawaguchi, Y., Nakamura, K., Tomonaga, M., 2020. Colour matters more than shape for chimpanzees' recognition of developmental face changes. Sci. Rep. 10 (1), 18201. https://doi.org/10.1038/s41598-020-75284-2.

Koopman, S.E., Allritz, M., McEwen, E.S., Dolins, F.L., Janmaat, K.R.L., Schweller, K., Call, J. (in press). *Chimpanzee turning behavior during spatial navigation in virtual environments*. Animal Behavior and Cognition.

Leinwand, J.G., Huskisson, S.M., Egelkamp, C.L., Hopper, L.M., 2020. Within- and between-species variation in the responses of three primate species to a touchscreen gambling task. Learn. Motiv. 71, 101635. https://doi.org/10.1016/j.lmot.2020.101635.

Martin, C.F., Biro, D., Matsuzawa, T., 2011. Chimpanzees' use of conspecific cues in matching-to-sample tasks: public information use in a fully automated testing environment. Anim. Cogn. 14 (6), 893–902. https://doi.org/10.1007/s10071-011-0424-3.

Martin, C.F., Biro, D., Matsuzawa, T., 2014. The Arena System: A novel shared touch-panel apparatus for the study of chimpanzee social interaction and cognition. Behav. Res. Methods 46 (3), 611–618. https://doi.org/10.3758/s13428-013-0418-y.

Martin, C.F., Muramatsu, A., Matsuzawa, T., 2022. Apex and ApeTouch: Development of a portable touchscreen system and software for primates at zoos (Article). Animals 12 (13), 13. https://doi.org/10.3390/ani12131660.

Matsuno, T., Tomonaga, M., 2007. An advantage for concavities in shape perception by chimpanzees (*Pan troglodytes*). Behav. Process. 75 (3), 253–258. https://doi.org/10.1016/j.beproc.2007.02.028.

Naik, H., Bastien, R., Navab, N., Couzin, I.D., 2020. Animals in virtual environments. IEEE Trans. Vis. Comput. Graph. 26 (5), 2073–2083. https://doi.org/10.1109/TVCG.2020.2973063.

Nölle, J., & Peeters, D. (To appear), *Virtual Reality: A tool to study language evolution.* In Raviv & Boeckx (eds.), The Oxford Handbook of Approaches to Language Evolution. Oxford: Oxford University Press.

Rapport Munro, E., Koopman, S.E., Anderson, S.P., Schweller, K., Röhr, H., Kleiman-Weiner, M., Lewis, R., Allritz, M., Robinson, L.M., Dolins, F.L., & Call, J. (in press). *Chimpanzees (Pan troglodytes) and Bonobos (Pan paniscus) Chase Prey Around Obstacles in Virtual Environments*. Journal of Comparative Psychology.

Ravignani, A., Sonnweber, R., 2017. Chimpanzees process structural isomorphisms across sensory modalities. Cognition 161, 74–79. https://doi.org/10.1016/j.cognition.2017.01.005.

Rumbaugh, D.M., Richardson, W.K., Washburn, D.A., Savage-Rumbaugh, E.S., Hopkins, W.D., 1989. Rhesus monkeys (Macaca mulatta), video tasks, and implications for stimulus-response spatial contiguity. J. Comp. Psychol. 103 (1), 32–38. https://doi.org/10.1037/0735-7036.103.1.32.

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

Schmitt, V., 2019. Implementing portable touchscreen-setups to enhance cognitive research and enrich zoo-housed animals. J. Zoo. Aquar. Res. 7 (2), 50–58. https://doi.org/10.19227/jzar.v7i2.314.

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

Sonnweber, R., Ravignani, A., Fitch, W.T., 2015. Non-adjacent visual dependency learning in chimpanzees. Anim. Cogn. 18 (3), 733–745. https://doi.org/10.1007/s10071-015-0840-x.

Stowers, J.R., Hofbauer, M., Bastien, R., Griessner, J., Higgins, P., Farooqui, S., Fischer, R.M., Nowikovsky, K., Haubensak, W., Couzin, I.D., Tessmar-Raible, K., Straw, A.D., 2017. Virtual reality for freely moving animals. Nat. Methods 14 (10), 995–1002. https://doi.org/10.1038/nmeth.4399.

Tomonaga, M., Imura, T., 2010. Pacman in the sky with shadows: the effect of cast shadows on the perceptual completion of occluded figures by chimpanzees and humans. Behav. Brain Funct. 6 (1), 38. https://doi.org/10.1186/1744-9081-6-38.

Wallace, E.K., Altschul, D., Körfer, K., Benti, B., Kaeser, A., Lambeth, S., Waller, B.M., Slocombe, K.E., 2017. Is music enriching for group-housed captive chimpanzees (Pan troglodytes)? PLOS ONE 12 (3), e0172672. https://doi.org/10.1371/journal.pone.0172672.

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

Wirth, S., Baraduc, P., Planté, A., Pinède, S., Duhamel, J.-R., 2017. Gaze-informed, task-situated representation of space in primate hippocampus during virtual navigation. PLOS Biol. 15 (2), e2001045. https://doi.org/10.1371/journal.pbio.2001045.