CHIMPANZEE (*PAN TROGLODYTES*) COGNITIVE MECHANISMS FOR JOINT ACTION AND VIRTUAL ENVIRONMENT NAVIGATION

Emma Suvi McEwen

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Emma Suvi McEwen

University of
St Andrews

This thesis is submitted in partial fulfilment for the degree of

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I, Emma McEwen, do hereby certify that this thesis, submitted for the degree of PhD, which is approximately 41,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for any degree. I confirm that any appendices included in my thesis contain only material permitted by the 'Assessment of Postgraduate Research Students' policy.

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Abstract

Chimpanzees have demonstrated across several experimental studies and field observations that they can successfully work together. The cognitive mechanisms that chimpanzees employ for joint action, however, remain unclear. A key component of human co-ordination is the ability to represent not only one's own role, but also the role of a partner. In the first two studies presented, I report evidence that chimpanzees may also represent a partner's actions during joint action. First, I present evidence that chimpanzees accommodate an experimenter's actions when passing an object, possibly incorporating another's actions into their own action plans. Second, I present evidence that chimpanzees learn about a partner's actions, which may facilitate their ability to produce those actions themselves in a partial role-reversal task. Another open question about chimpanzee joint action is the motivation behind choosing to work together or alone. To investigate whether physical effort may influence chimpanzees' apparatus choices, I present evidence from a task in which chimpanzees chose between a high and low effort puzzle-box apparatus. Chimpanzees showed no preference for either apparatus. There is also a spatial component to joint action, and how the action space is represented may affect perspective taking and how others' actions are represented. In the final experiment, I examined chimpanzee's spatial frames of reference in a virtual environment task. The results showed that some subjects used a simple landmark as an allocentric cue, but not more distal landmarks. Learning about how chimpanzees represent virtual spaces, and whether they could conceive of alternative perspectives, is an important first step towards virtual cooperative games with captive primates. The results of this thesis suggest that chimpanzees understand the role of their partner during joint action, may not reduce their own effort, are sometimes able to use simple virtual landmarks, and can find out-of-sight food in a virtual environment.

Chapter 1: General Introduction

1.1 Joint Action

1.1.1 Defining Joint Action

Joint action has been defined as two or more people coordinating their actions in space and time in order to bring about a change in the environment (Sebanz et al., 2006). Sebanz & Knoblich (2021, p. 138) state that "the next challenge for the field of joint action is to generate an integrated perspective that links coordination mechanisms to normative, evolutionary, and communicative frameworks". To this end, this thesis aims to begin integrating perspectives on joint action and present new evidence on coordination mechanisms within an evolutionary framework through studying one of our closest living primate relatives, chimpanzees, and to learn about the cognitive mechanisms involved in joint action in this species. As a first step, I will outline several current definitions of joint action and social coordination, and aim to draw parallels between these definitions.

Knoblich, Butterfill, & Sebanz (2011)

Knoblich et al. (2011) make a distinction between 'emergent coordination' and 'planned coordination'. 'Emergent coordination' refers to coordination occurring due to perceptual cues related to certain actions, without an action plan, and without a concept of a joint plan. 'Planned coordination' refers to coordination entailing representations of the desired outcomes of an action, consideration of the roles different agents play in achieving this goal, and planning one's own actions with these in mind.

Miss, Adriaense, & Burkart (2022)

Extending Knoblich et al. (2011)'s emergent and planned coordination definitions, Miss et al. (2022) define two stages of planned coordination: 'goal-directed, planned coordination I' which includes action co-representation and some awareness of the need for a partner, and ‘goal-directed, planned coordination II’ involving mutual representation of each other’s action plans, motives, and beliefs.

Knoblich & Sebanz (2008)

Knoblich and Sebanz (2008) present series of scenarios to describe levels of social interaction which increase in mechanistic complexity. In the first, most simple, scenario, agents are “intentionally blind”, that is, they are not representing the intentions behind their own or another’s actions. This level includes simultaneous affordance, which describes two or more agents acting in the same way due to environmental influences. For example, two people in a bar may simultaneously sip their drinks; these people are not acting jointly, rather they are both acting on the affordances of the props in their environment at the same time. This first level also includes entrainment, whereby two agents may act in temporal synchrony, such as falling into step when walking side-by-side. Here, agents’ actions may be somewhat influenced by the actions of another, but this form of ‘co-ordination’ does not necessarily require any interdependence of actions, planning with another’s actions in mind, or indeed any intention behind the co-ordinated movement. In scenarios 2 and 3, Knoblich and Sebanz (2008) describe simulating intentional action in another agent (scenario 2) and distinguishing between one’s own and another’s perceptions (scenario 3). Agents may be able to draw on their own action repertoire in order to simulate another agent’s action plan, and use this to inform their own motor plan when actions are interdependent. In the final, most complex level, agents are able to simulate another’s intentions, engaging some Theory of Mind mechanisms. Knoblich and Sebanz describe this framework for outlining human cognition as highly interactive rather than as isolated modules, and the simpler sensorimotor mechanisms described in the first level may be controlled by higher level mechanisms.

Pacherie (2013)

Pacherie (2013) posits that the following three requirements must be satisfied for an event to be considered joint action:

1.) Common outcome requirement: an event is the common outcome of multiple agents, not brought on by an individual.
2.) Individual intentional action requirement: the event is brought about by action[1].
3.) Common goal requirement: the agents aim for their actions to have the same overall outcome on the environment.

Pacherie goes on to extend this list of requirements to say that for actions to be truly *joint* (rather than what Butterfill (2012, p. 35) calls "plural activities") there is an additional requirement:

4.) Action coordination requirement: there must be coordination between the actions of the agents.

Pacherie specifies that some emergent coordination processes (Knoblich et al., 2011) could satisfy the conditions listed thus far. Continuing the extension of the requirements, for joint action to be *intentionally joint*, it must also meet:

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[1] Note that Pacherie here mentions intentionality which can be a controversial term in Comparative Psychology when talking about animal minds, and for some may exclude animals from reaching this criterion, but it seems the aim of this requirement is to exclude non-actions which could cause an outcome in the environment, such as sneezing.

5.) Intentional action coordination requirement: this can include using another agent as a social tool by understanding that another's actions can help to achieve your own goal, as that goal is shared.

If, for example, two agents use each other as social tools and coordinate to achieve a shared goal, Pacherie refers to this as 'shared intentionality lite'. The final requirement for *fully shared intentionality* is:

6.) the joint goal requirement: this is distinguished from previous requirements as having a truly shared goal, or goal of acting together, as opposed to independently having a goal that happens to be shared with another agent.

Michael, McEllin, & Felber (2020)

Michael et al. (2020) propose a minimal definition of coordination: "An agent is coordinating with another agent to the extent that she adapts her actions or decisions to the actions or decisions of that other agent, i.e., to the extent that she acts or decides as she does at least in part because of the observed or expected actions of the other agent" (Michael et al., 2020, p. 2). With this definition, Michael and colleagues specify that the action adaption need only be unidirectional to meet this minimal coordination criterion, that is, two agents do not need to both adapt to one another to be considered coordinated (although this can also be bidirectional), and there does not necessarily need to be a goal to the co-ordination.

Tomasello (2018)

Tomasello (2018) states that when non-human great apes (hereafter, great apes) work together, they do so in Tuomela's (2007) "I-mode"; that is, without joint goals, rather with only their own goal in mind (for example, to hunt a monkey). While Tomasello notes that great apes have evolved sophisticated socio-cognitive skills, he marks this as distinct from the ways in which humans collaborate. Humans, according to Tomasello, engage in "thinking for cooperating" and possess specific skills and motivations for co-operating, for example, through communication and shared intentionality, which is distinct from other great apes.

Tuomela (2007)

Tuomela (2007) makes a distinction between acting in "I-mode" and "We-mode" during joint action. Whilst agents can achieve successful collaboration in "I-mode", here they have only their own goals in mind, which may well align with the goals of others, but are not part of a broader collective. In contrast, "We-mode" is considered by Tuomela to be true cooperation, and is described as working as "cogs in a machine" (Tuomela, 2007, p. 175). Here, the motives of the whole group are in mind and there is trust that other members of the joint action team will also prioritise the goals of the group. It seems that parallels can be drawn between Tuomela's "We-mode" and Tomasello's "shared intentionality" as both require something additional to a successful coordination or cooperative behavioural outcome; both may require some greater social motivation and shared understanding between individuals that they will work together, and may require bidirectional intention understanding to know it is shared.

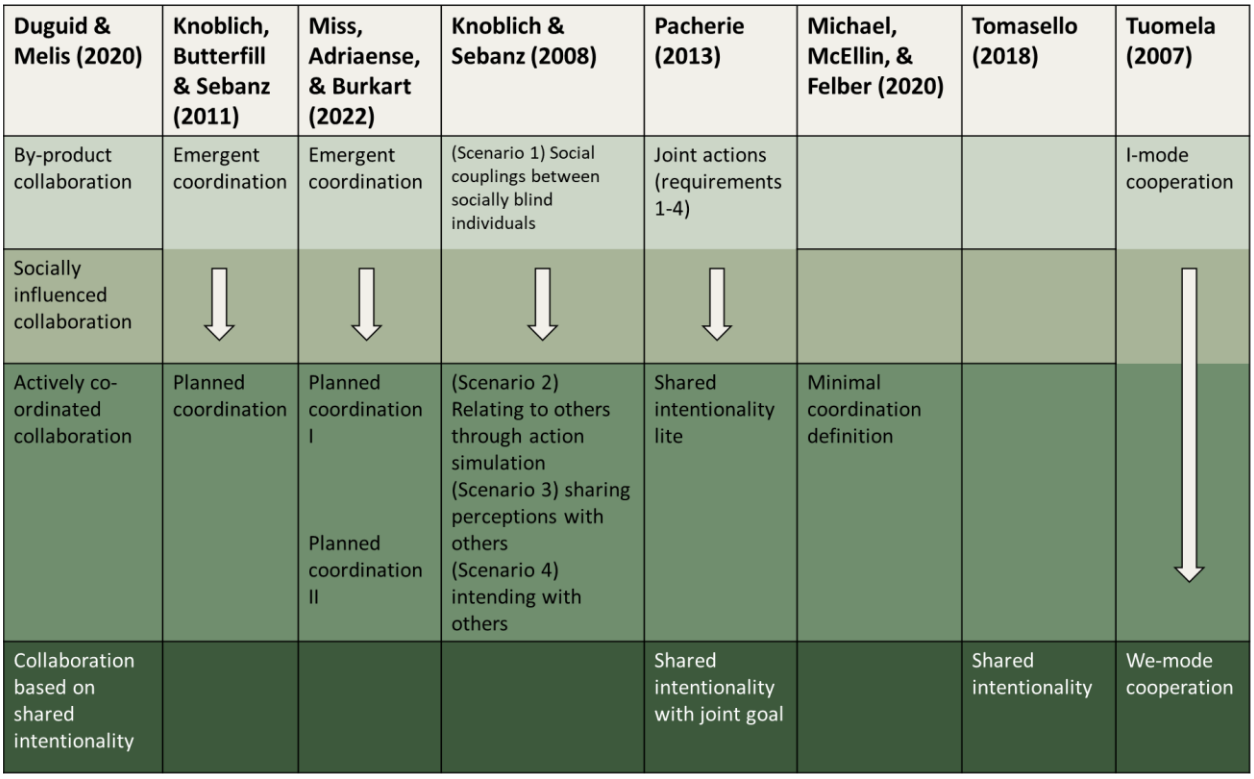
Duguid & Melis (2020)

Whereas the definitions listed thus far have largely focused on how humans work together, Duguid & Melis (2020, p. 4) describe categories of collaboration specifically to describe how non-human animals (hereafter, animals) may work together. At the simplest level is "by-product collaboration" whereby two or more animals may react to the same external cue, such as prey presence, and act independently, but perhaps in a complimentary manner, with the individual aim of acquiring the goal. This could include not adjusting to a partner's actions at all, and describes scenarios with no spatial coordination. The next category, "socially influenced collaboration" involves some impact of another agent, such as being more responsive towards an apparatus via social facilitation, but still not understanding the role they play in a task. This could include acting simultaneously, but with no intentional or flexible strategy. Beyond that, in the next category, "actively coordinated collaboration", animals may represent another agent's actions and possibly intentionally coordinate their actions in a task. This could include recruiting a partner, or aiding a partner's actions. Finally, the most cognitively sophisticated category described is "collaboration based on shared intentionality" in which partners intentionally coordinate actions and have mutual awareness that each other share a goal. Here, individuals could demonstrate communication of an intention to work together, or a commitment to shared goals.

Combining Definitions

Joint action has been studied and defined by many scholars, but there is often disagreement over what the term means and what levels of cognitive or behavioural complexity ought to be included under the term. There is a general lack of clarity and inconsistency regarding joint action research, which may prevent interdisciplinary, or indeed intra-disciplinary, collaborations and discussions, and could hinder attempts to understand the underlying latent variables (Miss et al., 2022; Milward & Carpenter, 2018). Drawing parallels between definitions is important to inform joint action research and to understand where similarities and differences lie in varying schools of thought. Pacherie (2011) points out that both minimalist and maximalist definitions may have pitfalls; minimalist definitions that attempt to encompass a broad range of interactions do not explain more complex aspects of joint action such as shared intentionality, whereas maximalist definitions may set the bar too high and exclude many interactions.

I will use and refer to Duguid and Melis' (2020) framework throughout this thesis as it captures a range of cognitive complexity across the levels and offers appropriate operationalised definitions for animal cognition work. As a first step, I have attempted to begin linking definitions and consider which levels of the definitions may have similarities. It is important to acknowledge that this is an oversimplified overview, and there are more nuanced differences and overlaps between the levels outlined here than the following figure would suggest (Figure 1).



Duguid & Melis (2020)	**Knoblich, Butterfill & Sebanz (2011)**	**Miss, Adriaense, & Burkart (2022)**	**Knoblich & Sebanz (2008)**	**Pacherie (2013)**	**Michael, McEllin, & Felber (2020)**	**Tomasello (2018)**	**Tuomela (2007)**
By-product collaboration	Emergent coordination	Emergent coordination	(Scenario 1) Social couplings between socially blind individuals	Joint actions (requirements 1-4)			I-mode cooperation
Socially influenced collaboration	⇩	⇩	⇩	⇩			⇩
Actively co-ordinated collaboration	Planned coordination	Planned coordination I Planned coordination II	(Scenario 2) Relating to others through action simulation (Scenario 3) sharing perceptions with others (Scenario 4) intending with others	Shared intentionality lite	Minimal coordination definition		
Collaboration based on shared intentionality				Shared intentionality with joint goal		Shared intentionality	We-mode cooperation

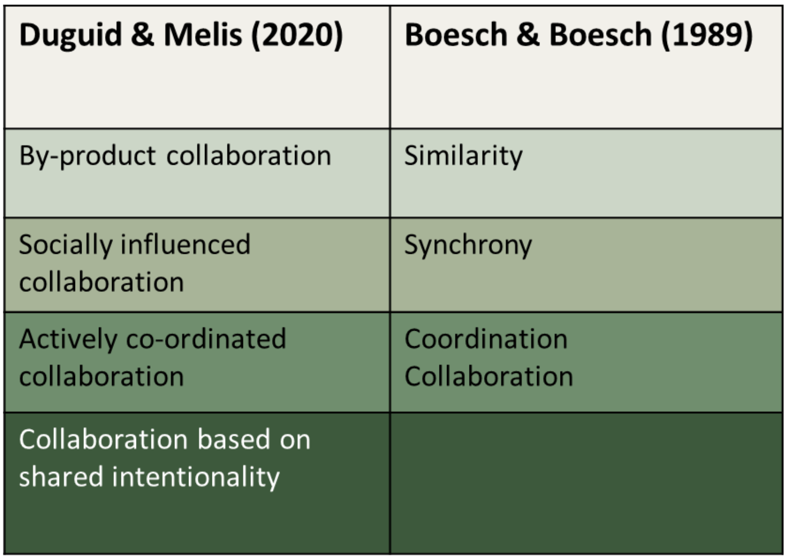
Figure 1: Overview of definitions of joint action, collaboration, and coordination. Different coloured bands indicate levels of cognitive complexity, increasing in complexity the further down the table they appear. Items in the same-coloured bands indicate similar levels of complexity, and/or similar behavioural indicators. Light arrows indicate that one level of a definition covers multiple bands, or levels of other definitions.

1.1.2 Joint action in non-human primates

Wild Chimpanzees

In the wild, chimpanzees engage in joint activities such as travelling together, patrolling the boundaries of their home ranges, and group hunting (Goodall, 1986; Wrangham, 1999; Boesch & Boesch, 1989). Wild chimpanzees use vocal communication to initiate joint travel, or to recruit others to join them in travel, wait, and check on travel partners, possibly indicating an intention to act together (Gruber & Zuberbühler, 2013). Further evidence of wild chimpanzees' cooperative skills is their consideration of group mates' knowledge states during vocal communication; they are more likely to communicate impending danger to groupmates who have not seen it themselves (Crockford et al., 2012).

Male chimpanzees also cooperate for aggressive encounters with outgroups, and form coalitions and alliances with in-group members, reinforcing social relationships with food-sharing and grooming, which can be reciprocal (Muller & Mitani, 2005). Such coalitionary behaviour has been seen across several chimpanzee communities and has fitness benefits such as maintaining high positions in dominance hierarchies and subsequently gaining access to resources and success in mating (Muller & Mitani, 2005). Although cooperative hunting of monkeys has been described for most hunts by chimpanzees in the Taï forest (Boesch & Boesch, 1989; Boesch et al., 2000), the same cooperative strategies have been challenging to find elsewhere and can be difficult to study, and so conclusions about the use of cooperation to hunt in chimpanzees are unclear (Muller & Mitani, 2005). Describing the ways in which chimpanzees in the Taï forest work together to hunt monkeys, Boesch and Boesch (1989) laid out four levels of increasingly complex strategies: Similarity (hunters acting in similar ways towards the same prey, with no spatial or temporal relations, for example, two hunters stalking the same prey); Synchrony (similar actions between hunters with some temporal coordination, for example, adjusting their speed); Coordination (similar actions on prey between hunters with some time and space consideration, for example, chasing from different directions and adjusting their positions with the other in mind); Collaboration (complementary actions towards the same prey, for example, one hunter chasing and another blocking their escape). Similarities can be found between these categories and the definitions outlined above. Figure 2 indicates where I suggest these descriptions could fit with the categories in Duguid and Melis (2020).



Duguid & Melis (2020)	**Boesch & Boesch (1989)**
By-product collaboration	Similarity
Socially influenced collaboration	Synchrony
Actively co-ordinated collaboration	Coordination Collaboration
Collaboration based on shared intentionality	

Figure 2: Overview of categories of collaboration from Duguid & Melis (2020) and descriptions of group hunting in wild chimpanzees from Boesch & Boesch (1989). Different coloured bands indicate levels of cognitive complexity, increasing in complexity the further down the table they appear. Items in the same-coloured bands indicate similar levels of complexity, and/or similar behavioural indicators.

Experimental evidence

The current evidence from chimpanzee joint action research suggests that it is at least “socially influenced” (that is, not simple “by-product collaboration”, Duguid and Melis, 2020). Chimpanzees are able to learn to wait for a partner before acting on a collaborative apparatus (Hirata & Fuwa, 2007) and demonstrate entrainment; when walking with a group-mate, they fall into synchronous gait patterns much like humans (Schweinfurth et al., 2022). The challenge comes with determining whether their collaborative behaviour reaches the criterion of “actively coordinated”, which requires intentional coordination and knowledge about a partner’s actions. In this section, I will briefly review the evidence of non-human primate (hereafter, primate) collaboration supporting this active coordination.

A classic paradigm for studying coordination between two chimpanzees is the cooperative tray pulling task, in which a chimpanzee dyad pulls ropes attached to baited trays so they both retrieve a reward each (Crawford, 1937; Melis et al., 2009). Chimpanzees have proven successful with several versions of this task, including when temporal coordination is required and when more than two subjects need to coordinate their actions (Hirata & Fuwa, 2007; Suchak et al., 2014). Although such paradigms are useful to determine if chimpanzees can spontaneously coordinate in this way, they often do not answer the question of how they do this and what cognitive mechanisms are driving this ability. Chimpanzees can learn to wait for a partner to be present before beginning to pull, demonstrating Duguid and Melis’ (2020) “socially influenced collaboration” (Hirata & Fuwa, 2007), and even selectively recruit coordination partners with whom they have had previous success, perhaps indicating Duguid and Melis’ “actively coordinated collaboration” (Melis et al., 2006). It could be argued, however, that alternative associative explanations based on reinforcement history with a partner have not yet been ruled out here. That is, it may be that subjects formed a mental link between specific individuals, the apparatus, and the successful outcome, without clearly understanding what role the partner plays. This association may have subsequently influenced their likelihood of recruiting those individuals when faced with the same apparatus. The cooperative tray pulling paradigm has been instrumental in demonstrating coordination in several species (Duguid & Melis, 2020), but the cognitive mechanisms employed to aid this coordination in chimpanzees remain unclear.

Another demonstration of chimpanzee cooperative ability is with the stag hunt paradigm. Here, a pair of subjects have the option to gain a low-value food reward (the hare) by themselves, or to forfeit this low value option in favour of a high value reward (the stag), for which they have to work together. If Subject A chooses to attempt the high-value cooperative option but Subject B does not, Subject A forfeits their chance of any reward. That is, both subjects must choose to cooperate for either of them to gain the high value reward stag. Within this paradigm, chimpanzees show a high rate of successful cooperation, often with one subject first risking leaving their hare, and the second subject following in response to either visual or auditory cues about the first subject's presence at the stag (Bullinger et al., 2011). This suggests that in this context, chimpanzees know that they need a partner to complete the task. In a later version of this task, in which the visual access to a partner was blocked and so the initial decision to leave the hare became riskier, chimpanzees were less successful coordinators (Duguid et al., 2014). A successful coordination strategy could have been communicating with their partner to coax them to the stag, a strategy used by children in the same study, but chimpanzees seldom attempted any communication here. It seems that chimpanzees use an actively coordinated strategy in this paradigm, as they seem to understand the need for a partner to be present at the stag (demonstrated by visual monitoring of the stag and their partner's hare) and often stay at their hare when they could not be certain that a partner would go to the stag. However, the low levels of communicative attempts to recruit a partner here are difficult to interpret. Furthermore, Silk (2009) points out that the stag hunt is a unique context (a "simple payoff scenario") as both agents involved have perfectly aligned motivations and so collaboration is the optimum choice for them both. In natural contexts, such payoff structures are not so unequivocal, and motivations and risks for each participant in a collaboration are rarely perfectly synchronised. In other settings, there are often competing interests, so observations of high levels of cooperation in the stag-hunt task may not generalise to other tasks or contexts.

Also included in Duguid and Melis' (2020) description of actively coordinated collaboration is "social tool use" in which an agent sees another as an actor in their goal achievement, and may use them as a means to an end to achieving their aim. Note that this would not necessarily require considering this other agent's goals or intentions, only that they can play an instrumental role in reaching one's own goal. Examples of this can be seen in Völter et al. (2015), in which orang-utan mothers physically manipulated their offspring to access food and had them fetch out of reach tools. Social tool use was also seen in Schweinfurth et al. (2018), in which a chimpanzee recruited group-mates to push out of reach buttons to release juice for him. In these cases, the subjects seemed to understand that other agents could be recruited or coerced into acting in service of their goal, without necessarily having a shared goal. Duguid and Melis (2020) point out that social tool use can in some cases be bidirectional, in which two agents may act together both in service of their own individual goals, using one another as pawns for their own gain, both benefiting from acting together but not conceiving of the goal as shared (see also Pacherie's (2013) fifth requirement above).

The Joint Simon task can offer insight into joint action representations (or co-representation) by looking at interference effects between two agents' actions (Sebanz et al., 2003). This interference effect was found in pairs of marmosets with responses to auditory stimuli, in which one sound associated with a left or right response was played either on its congruent or incongruent side of the testing station (Miss & Burkart, 2018).

When the task is joint, two individuals have one role each. An interference effect here suggests that one subject is representing both aspects of a task, as they incorrectly respond when their partner's role is cued. Such task co-representation could be indicative of Duguid and Melis's (2020) "actively coordinated collaboration". Miss et al. (2022) state that evidence from comparative work with primates suggests that co-representation may be a mechanism which is automatically activated when collaborating in a dyad. Marmosets, who are cooperative breeders and may thus have evolved more nuanced cooperative abilities (Burkart et al., 2014) also show increased vigilance when a feeding partner is occupied and unable to be vigilant themselves, and take turns to do so, showing consideration of what a partner is able and unable to do, and adjusting their own behaviour in turn (Brügger et al., 2023). It may be, however, that marmosets and humans have convergently evolved to be particularly cooperative, and this may not be shared across all primate species (Silk & House, 2016). More recently, however, the Joint Simon effect was also found in two more species of monkey (brown capuchins and Tonkean macaques), to a greater degree than the marmosets, and so task co-representation could be more common across primate species and warrants further exploration (Miss et al., 2022).

Other examples of chimpanzees actively coordinating include: passing tools to a partner, and, crucially, the correct tool of two options to complete a task (Melis & Tomasello, 2013); adjusting the view that a cooperative partner has of an apparatus differentially to a competitor (Grueneisen et al., 2017); and distinguishing between a task partner being unable or unwilling to continue in a joint task (Voinov et al., 2020). Whilst thus far, some evidence is emerging that chimpanzees can engage in actively coordinated collaboration, it is important to integrate this across more contexts and probe further into the cognitive mechanisms underlying chimpanzee joint action.

The evidence for collaboration based on shared intentionality in chimpanzees is, however, more scarce. Duguid and Melis (2020) suggest that communicating to initiate coordination may be evidence of this more complex form of collaboration but, thus far, across joint action studies, chimpanzees communicate very little (Duguid et al., 2014). Although Melis and Tomasello (2019a) observed chimpanzees possibly communicating information about a food location to a task partner by passing a tool in a location indicating where food was. This was, however, confounded with instrumental helping and perhaps task efficiency, as passing a tool at the goal location may be used to inform a partner, but also to aid action. While communicating a shared intention to collaborate may be an indication of cognitively sophisticated joint action mechanisms, it does not seem to be something that chimpanzees do readily (in Crawford’s early work, communication did not occur until approximately 90 sessions of a joint box pulling task; Crawford, 1937), nor do they necessarily use the information their partner may be trying to transmit (Duguid et al, 2020).

1.2 Spatial cognition

1.2.1 Linking the spatial and the social

Aspects of spatial cognition are evident in many of the definitions of joint action outlined above. In Knoblich and Sebanz's (2008) social interaction scenarios, the ability to distinguish one’s own from another’s perspective is deemed an important joint action mechanism, and spatial coordination is listed in Duguid and Melis’s (2020) “actively coordinated collaboration” and “collaboration based on shared intentionality” categories. Furthermore, many of the ways in which wild chimpanzees engage in joint action involve movement through space (boundary patrols, hunting) and learning about chimpanzee spatial cognition may provide insight into their social cognition.

In order to understand and make predictions about another's actions, and perhaps subsequently about their intentions, one needs to engage in spatial perspective taking (Creem-Regehr et al., 2013). Early research on the development of perspective taking abilities used the 'three-mountains' task in which children looking at a model mountain scene selected from pictures of a view which matched their own, and a view which matched a doll's view from a different location; a different perspective to that of the child (Piaget & Inhelder, 1956). Children aged 5-7 attributed their own view to the doll, failing to take their perspective and demonstrating an egocentrism. Later work with this paradigm, however, adapted the task demands and found that younger children (3-4 years) were able to correctly perspective take (Borke, 1975), and that a human actor instead of a doll also improved performance (Cox, 1975). Perspective taking ability has been linked to navigation ability in humans (Kozhevnikov et al., 2006).

1.2.2 Navigation (General)

Navigation has been defined as "co-ordinated and goal-directed movement through the environment [involving] […] both planning and execution of movements" (Montello, 2005 - p. 257). Navigation includes both locomotion (body movement) and wayfinding (planning and decision making with regard to the surroundings). Neural mechanisms such as place cells (but including several others) aid with this, which fire to inform an animal of where they are currently in their environment and their relation to other places (Montello, 2005; O'Keefe & Dostrovsky, 1971; Yoder et al., 2011). For several decades, questions have been asked regarding the nature of the mental representation of space that different animals have (Cheng & Jeffery, 2017). Tolman (1948) proposed the notion that animals use "cognitive maps", or internal map-like knowledge stores of space and configurations of their environment (Kitchin, 1994), evidenced, for example, by the ability to take short-cuts (when path integration and beaconing can be ruled out, Pritchard & Healy, 2017). Some view this idea as literal, in that the hippocampus is in effect a map, whereas others take a less literal viewpoint and interpret a “cognitive map” more as a metaphor or an analogy for how the brain makes sense of space (O'Keefe & Nadel, 1978; Kaplan, 1973; Kitchin, 1994). A cognitive, or Euclidian, map may be evidenced by integrating different experiences within the same environment into one representation, such as landmarks, rather than more simply associating a landmark with a target location without considering its spatial relations to more distal surroundings (Pritchard & Healy, 2017). The existence of cognitive maps is still debated, with some claiming to find evidence in wild animals (Bats: Tsoar et al., 2011; Chimpanzees: Normand & Boesch, 2009) and some suggesting it is more productive to ask how animals represent space rather than continue the search for human-like cognitive maps (Pritchard & Healy, 2017). Different species may use different spatial strategies during navigation and may learn about space differently, which may in part be shaped by feeding ecology (Rosati et al., 2014; Platt et al., 1996) or locomotion style (Davis et al., 2018).

1.2.3 Chimpanzee navigation

Chimpanzee navigation is complex, and many of the underlying cognitive mechanisms have thus far only been speculated about. Studies of wild populations have uncovered abilities such as memory for multiple food locations (Normand, Dagui, et al., 2009), goal directed travel to food sources rather than monitoring along the way (Janmaat et al., 2013), and efficient travel to food sources which minimize the overall travel distances (Ban et al., 2016). Furthermore, simulation of potential strategies using virtual maps has provided evidence that chimpanzees may use mental maps to find food sources (Normand & Boesch, 2009). Using these simulations, the detection fields of certain fruiting trees were varied to control for other strategies such as scent to detect these trees, but it was concluded that it was likely that mental maps were needed in order to locate these food sources. However, more controlled experiments are necessary to further investigate spatial cognition in chimpanzees and to uncover the cognitive tools they may be using to locate food sources in the environment. So far, controlled studies in captive settings have been limited in this area of study by restricted space and so recreating studies of real long-distance navigation have not yet been possible.

1.2.4 Virtual Environments

The use of computer technology in cognitive primate research has become increasingly popular over the last decade (Schmitt, 2019). Computerised testing allows for responses to be automatically recorded, offers tight control over stimuli presentation, and is engaging for members of public to observe (Egelkamp & Ross, 2019). Stimuli can be programmed to move and appear in novel ways, allowing for greater flexibility over what can be presented without the usual physical constraints inherent in non-computerised tasks. These methods can also ensure that stimuli are novel when subjects' prior experience may confound results. Furthermore, preliminary research has found that staff in a number of institutions positively evaluate the use of technology for research purposes in zoo settings (Clay et al., 2011). Continuing advancements in computerised testing systems and developments of new software could take the field of animal cognition into exciting new directions.

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 space. The tasks are often controlled by subjects' interactions or movements (feedback-based), meaning that subjects themselves decide when and in which direction to move (Dombeck & Reiser, 2012).

VE technology has advanced the study of animals in ways which would not have been practically possible with free-moving animals, such as neurophysiology in moths in a virtual flight simulator (Gray et al., 2002), and functional imaging of mouse hippocampal place cells during navigation (Dombeck et al., 2010). Research with some species has found similar behavioural responses to virtual and real-life stimuli, such as height aversion in mice and movement trajectories in drosophila and zebrafish (for a review, see Stowers et al., 2017). Similarities in responses to virtual and real-life environments have also been found on a neural level. Comparable place cell activity in virtual and real-life tasks has been shown in rodents (Harvey et al., 2009) and place-related neural responses during VE tasks have been shown in monkeys (Hori et al., 2005). The studies listed here suggest that VEs could be useful research tools with valid applications to animal behaviour.

More recently, VEs have been used as a non-invasive method of studying cognition in primates (Dolins et al., 2014). Dolins and colleagues presented chimpanzees with interactive three-dimensional maze environments on computer screens. The apes used joysticks to navigate through these mazes and were able to learn to use virtual cues to travel to reward locations and showed, in one case, more efficient routes than human participants. More recently, Allritz and colleagues (2022) found that chimpanzees could locate hidden food in a more naturalistic, open-space VE presented on a touchscreen. In their task, chimpanzees learned over the course of 14-18 days of testing to associate a landmark (a large tree) with food and to navigate to this landmark when starting from varying starting positions within the arena. This included cases in which the landmark was not visible at the beginning of the trial because, for example, the subject was facing in the wrong direction. The chimpanzees increased their path efficiency over time in some conditions. Subjects also learned very quickly the location of a second landmark tree that only sometimes bore fruit, and foraged with increasing flexibility, rejecting the more familiar landmark if it was seen to not be baited, in favour of the second one. In sum, research has begun to show that VE tasks are a viable method with which to study primate cognition.

1.3 Thesis Aims

This thesis investigates the cognitive mechanisms employed by chimpanzees during joint action in coordination tasks and in virtual environment navigation. I have been interested in action representation (studied through accommodation and action learning), motivation, and how virtual spaces are represented. I present four experimental chapters, outlined below, before closing with a general discussion of my findings and reflections, and my thoughts on future directions.

In Chapter 2, I present evidence from a tool handover task looking at action accommodation, which is a signature of human joint action. The chimpanzee subject was tasked with passing a stick tool to an experimenter across a series of experiments, each including different constraints on the experimenter's actions. I aimed to elucidate whether or not chimpanzees incorporate a task partner's actions into their own motor plans, and pass an object in such a way that incorporates the experimenter's action ease and capability. This takes inspiration from human literature on accommodative object passing and questions of action co-representation. In Chapter 3, I present a partial role-reversal task. Here, chimpanzees experienced a two-action task: in one condition, the first action was performed by a human cooperative partner; in the other condition, the first action was caused by a falling object. In both conditions, chimpanzees performed the second action. In a test stage, the first action did not happen, and I looked at whether chimpanzees in the cooperative condition performed the first action more than chimpanzees in the non-social condition, which could indicate that they had represented their partner's action.

In addition to action representation, I became interested in social motivation in chimpanzees as, while they are often successful co-operators, research suggests that working with a partner is not always their preferred solution, and they rather work alone. In Chapter 4, I look at the impact of task effort and efficiency on chimpanzees' choices to engage with an apparatus. If chimpanzees are motivated to reduce their effort, or choose efficient actions, it follows that this may factor into their choices to work alone.

In my final experimental chapter, Chapter 5, I present evidence from a recently developed method for studying primate cognition: virtual environments. Here, I was interested in validating this method further by investigating how virtual spaces are represented by chimpanzees, as well as learning more about their use of spatial frames of reference.

Chapter 2: Chimpanzees demonstrate a signature of human joint action[2]

Summary

Effective social co-ordination benefits from mentally representing a partner's actions. Humans optimize social coordination by forming internal action models adapted to joint rather than individual task demands. Such co-representation is seen during handover tasks; objects are passed in ways that facilitate the action to be performed with them. For example, an object may be passed in such a way that a partner can easily and comfortably grasp it. Chimpanzees are able to plan their own actions to benefit their own individual needs and preferences, but do chimpanzees also consider the joint action sequence? I present a joint handover-to-retrieve task across six experiments to assess whether, like humans, chimpanzees incorporate a task partner's actions into their own action plan. I manipulated my hand location, action capability, and action ease, and then assessed the location in which chimpanzees passed me a tool. I found evidence that chimpanzees accommodated a task partner's actions relative to a receiver's hand location and action ease. These findings reveal that chimpanzees are attentive to the predicted actions of a task partner and may share common cognitive mechanisms with humans that support joint action.

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[2] This project was a collaboration with Merryn Constable, Günther Knoblich, Callum Gibson, Amanda Addison, and Sophia Nestor. A version of this has been submitted for publication and is currently under review.

Introduction

Joint action in humans

Humans have the ability to fluidly coordinate and adapt to a coordinative partner's needs. This ability allows humans to successfully share tasks and work jointly, which is a key aspect of human life. Although humans often do this with relative ease and with infrequent coordinative failures, the cognitive processes that may be deployed for efficient interactions can be quite complex. This tendency to collaborate and coordinate can be considered a potential evolutionary advantage for the human species (Tomasello, 2014), as humans have a range of mechanisms in their cognitive tool-kit that may be engaged to support effective coordination (Sebanz & Knoblich, 2021). The present study asks whether the cognitive mechanisms that have evolved in humans to achieve smooth and successful coordinative outcomes can also be observed within chimpanzees. Specifically, do chimpanzees represent the actions of a human co-agent in a joint handover-to-retrieve task?

Humans form internal models during action planning, which can adapt to various aspects of the environment or task (Wolpert et al., 1995). These models provide a prediction of action possibilities and a plan for the best course of action to achieve a goal relative to environmental demands, and are continually updated and adjusted based on experience. For example, consider picking up a bucket that you believe to be full. The expected weight of the bucket is integrated into our internal action models; we proactively plan for the expected sensory feedback. If we find that reality contrasts with our prediction, for example, if the bucket is much lighter than we expected, we have to update these models and adjust our actions to react to the new information and sensory feedback (Miall &

Wolpert, 1996). Internal models provide scaffolding for action, but can be adjusted when the sensory experience does not match the prediction.

In social settings, humans can use internal action models to predict another agent's behaviour (Vesper et al., 2013), and integrate another agent's possible actions into these predictive action plans. In fact, humans show similar motor preparation in the brain for joint actions (with another agent) and bimanual independent action (Kourtis et al., 2014); we include other's actions into our models as well as our own. Humans can thus create shared representations between co-agents that consider joint tasks as a whole (co-representation) (Pezzulo, 2011; Sebanz & Knoblich, 2021). This is evidenced by selecting actions that maximise the efficiency of joint goals over individual components of tasks (Curioni et al., 2022; Török et al., 2019). This establishment of tasks and goals as shared is thought to be a critical component of the way in which humans optimize coordinative episodes (Pezzulo, 2011; Sebanz & Knoblich, 2021).

Joint action in primates

Similar to humans, primates demonstrate behaviour consistent with using internal predictive models for action sequences. For example, the End-State Comfort Effect – the tendency to grasp an object in a way that ensures that the final orientation of the item is comfortable (Rosenbaum & Jorgensen, 1992) – can be observed in lemurs (Chapman et al., 2010), chimpanzees (Frey & Povinelli, 2012), cotton-top tamarins (Weiss et al., 2007), and brown capuchin monkeys (Zander & Judge, 2015). Thus, evidence points to predictive action planning on an individual level, but can such action planning effects be found in a joint context, as in humans? Investigating action representations during joint tasks may uncover the cognitive complexities of chimpanzee social coordination.

As illustrated above, shared representations are thought to be necessary for successful joint action in humans (Pezzulo, 2011). Common marmosets exhibit co-representation effects (Miss & Burkart, 2018) and chimpanzees selectively recruit coordination partners with whom they have had previous success, indicating some understanding of a task partner's role (Melis et al., 2006). Also, chimpanzees alter the visibility of their actions differently to co-operators and competitors, indicating perspective taking during interactions (Grueneisen et al., 2017). Similarly, chimpanzees and bonobos position themselves within an experimenter's field of view to visually gesture for food (Liebal et al., 2004). Byrne (2002) suggests that great apes are likely to perceive action plans in others, due to their performance in imitation tasks in which they may detect "program level" plans of action. Thus, it is plausible that chimpanzees also possess cognitive processes that support joint action beyond minimal forms of non-intentional "emergent coordination" (Knoblich et al., 2011).

The Present Study

If chimpanzees can flexibly adapt their actions in response to a co-agent's actions, it would suggest that their internal models for action represent the expected motor states of their co-agent. Such a finding would provide evidence of a system that supports joint action planning in chimpanzees. I therefore developed a joint handover-to-retrieve task reflecting an approach to studying joint action in both humans and. In human handover tasks, participants typically orient objects so that a co-agent may more comfortably grasp or interact with that object, termed the 'Beginning State Comfort Effect' (Constable et al., 2016; Gonzalez et al., 2011; Ray & Welsh, 2011). For example, passing a mug with its handle facing the direction of a partner, or holding the blades of a pair of scissors so the receiver can grasp the handle. This drive towards considering the interaction needs of a partner is evident from a young age in humans (Meyer et al., 2013) and may be adjusted to the action capabilities of the partner, as well as the difficulty of the task (Ray et al., 2017).

The Beginning State Comfort Effect, however, may not directly represent the facilitation of a co-agent’s action. Török and colleagues (2019) demonstrated that when transferring a virtual object to a co-agent, participants favoured co-efficient paths that minimized the aggregate costs of movement for the dyad rather than routes that minimized the costs for only themselves or their co-agent. Thus, although accommodating another’s action often looks altruistic, the effect is better explained by the maximization of co-efficiency (Strachan & Török, 2020; Török et al., 2019, 2021).

The present task was designed to conceptually mirror extractive foraging, which is commonly observed in wild chimpanzees (McGrew & Rogers, 1983) and orang-utans (Meulman & van Schaik, 2013), and all great apes (Mulcahy & Call, 2006) and capuchin monkeys (Visalberghi et al., 1995) in captive settings. Moreover, in social contexts, orang-utans pass tools to partners to obtain food (Völter et al., 2015). Furthermore, chimpanzees and bonobos pass tools to conspecifics, mainly when help is requested (Yamamoto et al., 2012; Nolte & Call, 2021), sometimes even changing the location where they give a tool to a partner based on a reward’s location (Melis & Tomasello, 2019). These studies have shown that non-human apes (hereafter, apes) can use others as 'social tools' to achieve a goal, will instrumentally help a partner accomplish a goal, and show some flexibility in the location in which they pass tools. Thus, a tool-based extractive foraging task was chosen for ecological validity and because great apes pass tools to one another in experimental settings. The chimpanzee subject was provided with a stick tool which they needed to pass through a window to me. I would then extract pieces of fruit from transparent tubes to give to the chimpanzee. Across several studies, I systematically investigated the extent to which chimpanzees incorporated a co-agent’s action into their overall action plan.

Experiment 1 tested whether chimpanzees' passing locations were influenced by where I placed my hand behind a mesh window that provided the chimpanzee with the freedom to pass at any location. If chimpanzees attended to or accounted for the location of my hand while passing, I would expect that they would demonstrate flexibility in passing locations relative to where my hand was placed, as indexed by a shift in passing location towards that hand.

To rule out attentional explanations, Experiment 2 investigated if chimpanzees accounted for my action capabilities. In this case, I presented both hands, but one hand was occupied by a walkie-talkie, thus preventing me from grasping the stick with that hand. If the chimpanzees understood that I could not grasp with the occupied hand and accounted for the fact that I would have to grasp the stick with my free hand, then we should observe a shift in passing location towards that free hand.

The first two experiments focused on chimpanzees’ responses to differences in the experimenter’s action capabilities. Humans also alter their internal joint action models in response to the action ease of a co-actor (Schmitz et al., 2017). Thus, Experiment 3 investigated whether chimpanzees incorporated my action ease: a barrier that I had to reach over was present on one side of the window. Critically, I could use both hands, but my actions were more efficient when I used the hand that was not obstructed by the barrier than when I used the hand that was obstructed by the barrier. In Experiment 3A, the subject was provided with a binary choice between passing locations: my obstructed side vs my unobstructed side. Experiment 3B used the same barrier but with the mesh window to provide a continuous measure of passing location similar to Experiments 1 and 2. If chimpanzees account for the ease of my action, we would expect them to pass at a location closer to the unobstructed hand.

In Experiment 4, I tested whether the chimpanzees would adapt their action preferences in a binary choice situation when action in one location was made impossible by an inaccessible box. This experiment also examined the effects of the box's properties: the box was opaque in Experiment 4A and transparent in 4B. If chimpanzees understood how the box influenced my action capabilities and incorporated that understanding into their action plans, then they would not pass to the obstructed side in Experiments 4A and 4B.

Methods

Subjects

Twelve chimpanzees participated in this study (7 females and 5 males, mean age 29.6 years [SD = 13.3, range = 4-46 years] at the beginning of data collection), shown in Table 1.

Table 1: Subject demographic information.

Name	**Group**	**Sex**	**Age (years)**
David	EDI	M	44.2
Frek	EDI	M	25.5
Liberius	EDI	M	20.2
Velu	EDI	M	4.8
Eva	EDI	F	38.4
Kilimi	EDI	F	26.2
Alex	LPZ	M	19.0
Frederike	LPZ	F	46.2
Swela	LPZ	F	26.1
Fraukje	LPZ	F	45.6
Dorien	LPZ	F	41.1
Kisha	LPZ	F	17.7

Six chimpanzees were housed at the Budongo Research Unit (BRU) in Edinburgh Zoo, Scotland, and six were housed at the Wolfgang Köhler Primate Research Centre (WKPRC) in Leipzig Zoo, Germany. All chimpanzees lived in a social setting with access to climbing structures, foraging boxes, and seasonal (Leipzig) or daily (Edinburgh) access to outdoor enclosures. On each testing day, access was made available to a testing room. Subjects were given the option to enter and participate in cognitive tasks to earn food rewards additional to their regular diet. 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. In Leipzig, individuals were separated for testing (with the exception of mothers and dependent offspring), and in Edinburgh, subjects were tested with other group members present.

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 BRU committee, consisting of the Zoo Research Liaison Officer, the Scientific Director, and the Research Coordinator. Research in Leipzig was approved by the WKPRC committee composed of the director of WKPRC, the research coordinator, the head keeper of great ape husbandry, and the zoo veterinarian. The research was also approved by the School of Psychology and Neuroscience Research Ethics Committee at the University of St Andrews.

Apparatus

Chimpanzees were given the opportunity to approach a window (approximately 62cm x 74cm) which was either open mesh (Experiments 1, 2, 3B) or clear polycarbonate with two holes (approximately 4cm in diameter, Experiments 3A, 4A, 4B) in their testing area. On a table on my side of the window was an apparatus consisting of three open-ended, transparent plastic tubes mounted onto a piece of wood and baited with fruit (pieces of grape) via a hole in the top (see Figure 3). A stick was required to retrieve the grape pieces by pushing them out of the tube, which could be done via either opening. In Experiment 1 (Hand Location Task), no additional materials were used. In Experiment 2 (Obstructed Hand Task), I held a walkie-talkie in one hand. In Experiment 3 (Barrier task), I placed a three-sided, transparent polycarbonate barrier on the table on my side of the window and pushed this against the testing window. The barrier was 50cm tall, 37cm wide (approximately half the width of the testing window) and was 32cm away from the window. I piloted a shorter version of the barrier (21.5cm tall) with 4 chimpanzees before settling on the taller barrier. In Experiment 4 (Box Task), an opaque wooden box (4A) or a transparent polycarbonate box (4B) replaced the barrier used in Experiment 3. The boxes were 35cm^3, with one side open. I pushed the open side against the testing window such that a subject could pass a stick to that side.

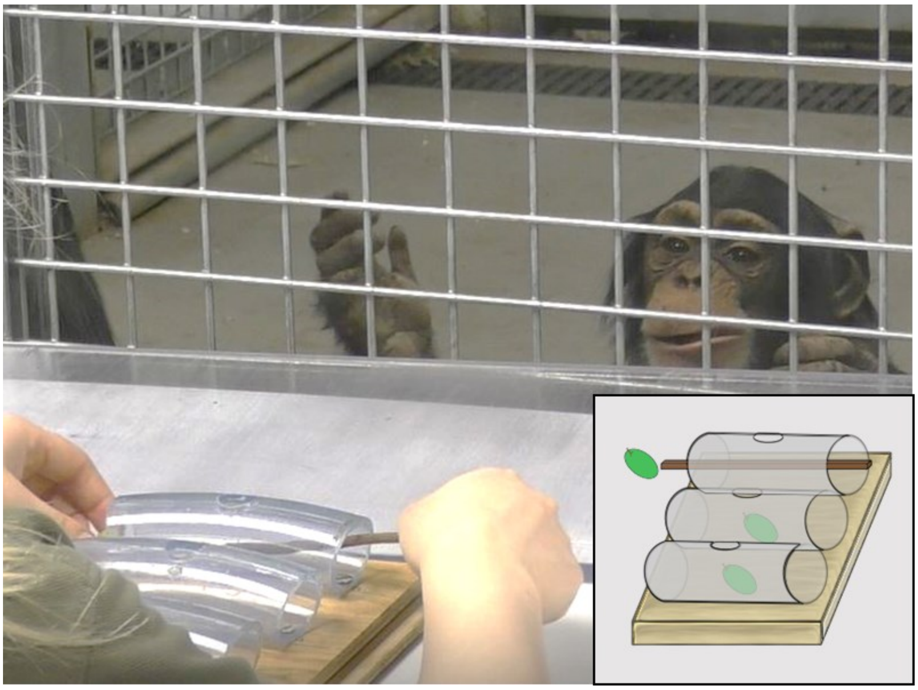

Figure 3: Chimpanzee (male, Velu) engaging in the handover task. Inset depicts the baited tubes. To retrieve the grape pieces, I needed to insert the stick and push them out.

Procedure

General procedure

Once a subject sat attentively in front of the testing window, I transferred a stick down a central plastic tube leading to the floor in front of the subject. After I gave the subject the stick, I placed one or two hands (depending on the experiment) in front of the mesh and asked for the stick (“give me the stick”). In some cases, I used the chimpanzee’s name during the request to gain attention. Once I had grasped the stick (either with the hand closest to the passing location, or with my available hand [E1 and E2]), I used it to retrieve the pieces of grape for the subject using that hand (i.e., the side that the grape pieces were pushed from differed depending on the hand I used). Each experiment consisted of 12 trials per subject. Subjects were rewarded regardless of where they passed the stick, other than in Experiment 4 which was differentially reinforced, as sticks passed into the box were then inaccessible to me.

In Experiments 1 and 2, I pseudo-randomised open hand locations with no more than three of the same trial types in a row. In Experiments 3 and 4, I used a counterbalanced blocked design such that the side of the barrier or box was changed after 6 trials, and the starting side was randomized between subjects. This was to avoid moving the apparatus between individual trials. In experiments with the mesh window, when my hands were placed on the left and right sides these were approximately two mesh squares from the edge. In experiments with the polycarbonate window, the two holes were at approximately the same locations as where I had held my hands in the mesh experiments.

In Experiment 3, I waited 5 seconds after the chimpanzee had begun passing the stick (from when the stick was approximately halfway through the window) before using it. This wait time was implemented to account for the difference in time between the handover and reward retrieval when the pass was made to the barrier side vs the open side. Thus, the amount of time that the chimpanzee would wait before receiving the reward was equalized regardless of where they chose to pass the stick. I performed Experiment 3B between Experiments 4A & 4B because 3B was a later addition to the already planned series of experiments.

Pre-tests

Subjects underwent two pre-tests before the experiment to determine if they would pass a stick to me and if they responded to gestural cues to pass a stick.

Pre-test 1 (hand orientation): The aim of the first pre-test was to assess whether an up-turned hand would be differently responded to than a down-turned hand as it is possible that an up-turned hand might carry more weight as a request.

Once I gave a stick to a subject, I placed my hands equidistantly away from the sides of the window (approximately two mesh squares from either side) with one palm facing up and one palm facing down. I pseudo-randomised and counterbalanced orientation with no more than three of the same trial type in a row. I made a verbal request for the stick and slightly moved my hands up and down indicating a request. I would grasp the stick if it was inserted through the mesh with the hand that was closest and then retrieve the grape to give to the subject. Subjects completed a series of 12 trials, if they did not successfully pass the stick on 10 trials, they would complete another 12 trials until they reached the threshold. Three subjects completed an additional 12 trials despite meeting the threshold because the window used for testing was changed. One repeated PT1 immediately, the other two moved to PT2 before repeating PT1. One subject required a second round of 12 trials and two required additional husbandry training with animal care staff to learn to pass the stick (see details below), and three rounds of PT1 in total. The remaining 6 subjects met the threshold within 12 trials. For all subjects, their final session (12 trials) of PT1 is reported.

Training: If subjects passed the stick on fewer than half of the trials in the first pre-test then they were moved to a training stage in which they were trained to trade a stick for a grape. Training was passed when a stick that was dropped down the tube was traded with animal care staff for a grape in 12 trials.

- Two subjects completed the training phase and then moved back to the experiment
- One subject moved to the training phase but never learnt to pass the stick and thus did not progress to the experiment.

- Two subjects moved to the training stage and then back to the pre-test, but did not participate or pass the stick frequently enough to progress further within the time frame allocated for testing.

- Two subjects completed both pre-tests but subsequently participated too infrequently and so did not progress.

- One subject completed part of the first pre-test but participated too infrequently and thus did not progress further.

Pre-test 2 (passing to one open hand): After I gave the stick to the subject, I placed one hand centrally in front of the mesh. I pseudorandomised the hand used (left or right hand) with no more than three of the same trial types in a row. I would grasp the stick with the hand I placed in front of the mesh and then retrieve the grape to give to the chimpanzee. The pre-defined pass criterion was to give the stick to me within 10 seconds in at least 10/12 trials, but subjects were rewarded for all trials in which they passed the stick regardless of the time taken. All subjects reached the pass criterion in one session.

Procedure for each experiment:

- Experiment 1 (Hand Location Task): Hand left side, central, or right side behind the mesh. For left and right location, the corresponding left and right hand was used. For the central location, the hand (left or right) was counterbalanced and placed centrally.

- Experiment 2 (Obstructed Hand Task): Two hands facing sideways (one on the left and one on the right) behind the mesh, palms facing one another. A walkie-talkie occupied one hand.

- Experiment 3 (Barrier Task): A transparent barrier obstructed one side of the window. Hands were upward facing on left and right sides behind a polycarbonate (3A) or mesh (3B) window. I placed both hands further back due to the presence of the barrier.

- Experiment 4 (Box Task): An opaque (4A) or transparent (4B) box prevented my access to one hole in the polycarbonate window. My hands were facing upwards on left and right sides behind the window holes and box. With the opaque box, I raised my hands, so the box did not obstruct the subjects' view of them. With the transparent box, my hands were at the same height as the holes in the polycarbonate window and I placed both hands further back due to the presence of the box.

An example video can be found for each experiment via the following link: https://osf.io/bnhzr/?view_only=31dcc570450a423da23208fcfca21cc3

Data Processing

I coded all passing locations from video recordings. Importantly, I coded data based on the initial location selection by the subject rather than the final location selection, because I took this to be reflective of the initial action selection rather than any adjustment based on the sensory consequences of their action. That is, if a subject began passing the stick in one location, but subsequently switched to a different location, I coded the data of the initial location (see supplementary video for an example of such a location switch). Location switches happened very rarely.

I used windows that differed in terms of the spatial layout of the mesh when testing at different locations. For appropriate data analysis, I equalized these. Both types of mesh windows had ten squares along the vertical dimension. I coded these from 1-10, bottom to top. The mesh differed along the horizontal dimension: one type of window had 14 squares and the other 13. I equalized the horizontal mid-point to 0. Thus, for the window with 13 squares, the middle square was 0, whereas for the window with 14 squares, the two middle squares were -0.5 and 0.5. This convention ensured that the location from the centre was accurately mapped between the windows. Therefore, a positive value represents a bias for the subject to pass to their right, and a negative value represents a bias for the subject to pass to their left.

A research assistant separately coded a subset of the data (13 of 96 total sessions across subjects; note that the 13 sessions were taken from 8 of the 12 subjects). I evaluated consistency in coding using Cohen's κ for judgements on the side selected in binary choices and found a very high degree of consistency: $\kappa = 1$, $p < .001$. I also found a high degree of consistency for the coding of vertical and horizontal dimensions, using interclass correlation (ICC): ICC = 0.963, $p < .001$ and $\kappa = 0.929$, $p < .001$, respectively. Note that during video coding, due to the issue with different sized windows outlined above, horizontal passing locations were labelled with letters for coding purposes and re-coded later for analyses (see above).

Data analyses

I completed all analyses in R (version R-4.0.2). Data were submitted to generalized linear mixed models (GLMMs), or linear mixed models (LMMs) if they were approximately normally distributed, using the *glmer* function with the bobyqa-optimiser for GLMMs and *lmer* function, all included in the “lme4” package (Bates et al., 2015). In all cases, I began with maximal models including random slopes and interaction terms of interest. In cases of non-convergence or singularity, random slopes were removed. Interaction terms of interest were included in the models, but were removed if they did not reach significance at the 5% level. I then compared full models to null models with the variables of interest removed using the *drop1* function. Variables were assessed for collinearity using the *vif* function in the *car* package (Fox et al., 2012) and in cases in which the Variance Inflation Factor (VIF) exceeded 3, one of the collinear variables was removed (Johnston et al., 2017), (VIF values can be found in Appendix C, Tables C1-C4). Effect sizes (odds ratios, estimated trends, and Cohen's *d*) were calculated using the *emmeans* package (Lenth et al., 2019). Currently, *emmeans* does not support Gamma models as they cannot be back-transformed to an interpretable scale, and so for these data the effect sizes are unavailable (emmeans package, Version 1.8.5, 2019). I created all data visualisations using the *ggplot2* package (Wickham, 2016). To account for slight differences in sizes of mesh and heights of holes between zoos, I included group (Edinburgh or Leipzig) in all models. I z-transformed the continuous variable 'trial' to normalise the data, and dummy-coded binomial variables as 0 and 1 to allow for clear comparisons.

Results

Pre-test 1

Passing Location: Because the criteria for successful completion of this task was passing on 10 out of 12 trials, I only submitted the last block of 12 trials to inferential statistics. There were two trials on which specific location data was missing. I observed no difference in passing location in relation to the location of the upward and downward facing hands along the horizontal dimension [pass location ~ hand orientation + trial + group + (1|Subject)]: χ2

(1) = 0.01, *p* = .92; no effect of group: χ2 (1) = 0.02, *p* = .88; and an effect of trial: χ2 (1) = 4.06, *p* = .04.

Pre-test 2

All subjects passed the stick on all trials except for one chimpanzee who did not pass on one trial. Three other subjects passed the stick outside of the 10 second window on one trial each. On average, chimpanzees took 2.53 seconds (SD = 3.49 seconds) to pass the stick.

Experiment 1

Horizontal passing location

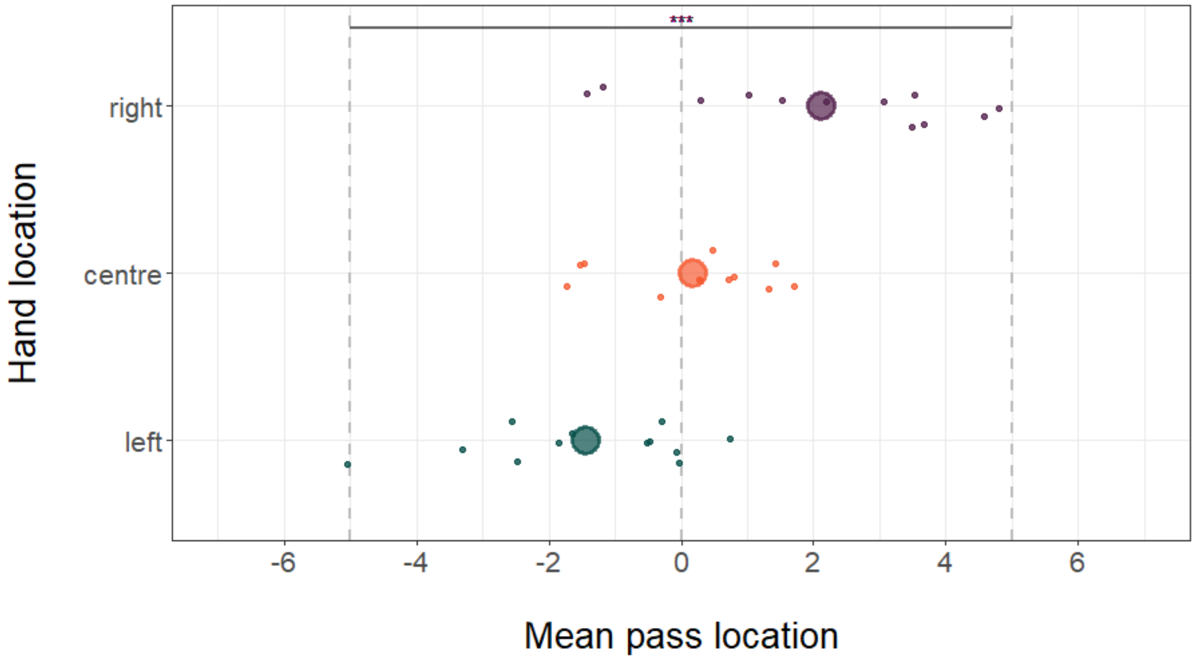

Figure 4: Average horizontal passing location for Experiments 1 as a function of the location of the experimenter's presented free hand. Large circles indicate the sample mean. Small circles represent each chimpanzee's mean. Grey dashed lines represent the approximate locations of the presented hands. From the chimpanzee's perspective, a negative value represents an average shift to the left, and a positive value represents an average shift to the right relative to the midpoint.

Experiment 1 – Hand Location Task: An LMM [pass location ~ experimenter hand location + trial + group + (1|subject)] revealed a significant effect of experimenter's hand location on chimpanzee's passing locations: χ2 (2) = 74.82, $p < .001$ ($d_{\text{central hand}}$ = 0.09, $d_{\text{left hand}}$ = 0.82, $d_{\text{right hand}}$ = 1.20). No effect of trial was found: χ2 (1) = 0.69, p = .41 and no effect of group (Edinburgh or Leipzig): χ2 (1) = 0.01, p = .94. As can be seen in Figure 4, when my hand was on the subject's left, the selected passing location was significantly further towards the left, and when my hand was on the right, the passing location was also significantly further towards the right. Thus, the location in which chimpanzees passed the object through the mesh shifted towards the location at which I presented my hand.

Experiment 2

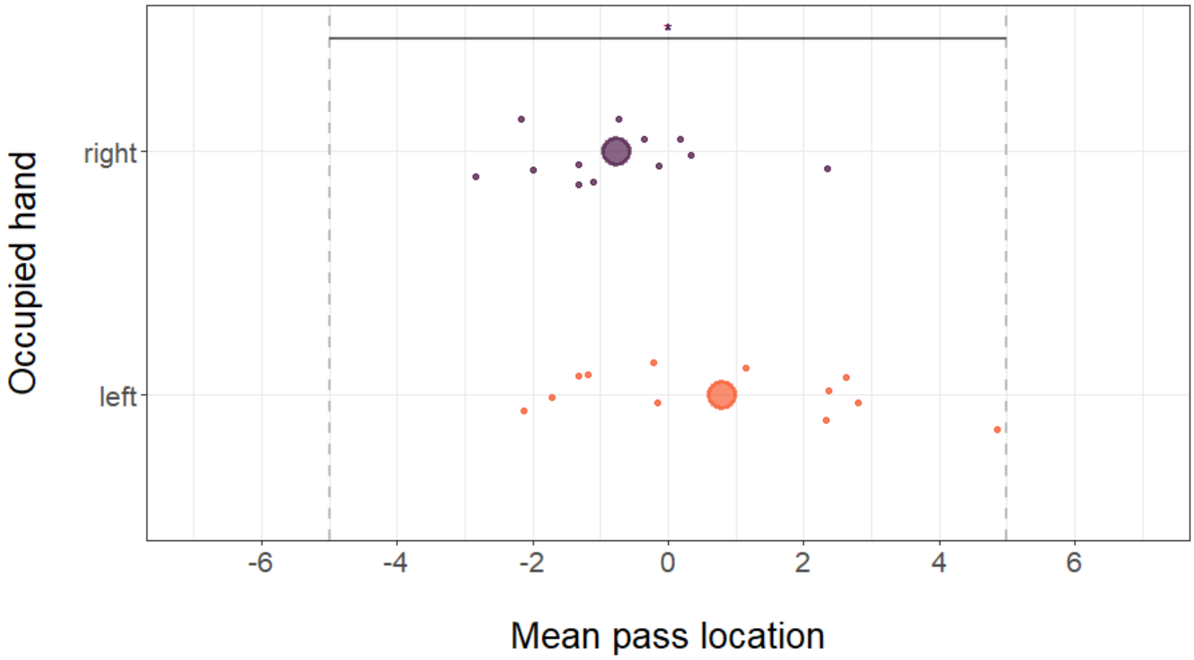

Figure 5: Average horizontal passing location for Experiments 2 as a function of the location of the experimenter's presented free hand. Large circles indicate the sample mean. Small circles represent each chimpanzee's mean. Grey dashed lines represent the approximate locations of the presented hands. From the chimpanzee's perspective, a negative value represents an average shift to the left, and a positive value represents an average shift to the right relative to the midpoint.

Experiment 2 – Obstructed Hand Task: An LMM [pass location ~ occupied experimenter hand + trial + group + (1|subject)] revealed a significant shift in passing location toward the experimenter's free hand, or away from the experimenter's occupied hand (Figure 5): χ2 (1)

= 17.22, *p* < .001, *d* = 0.71. I found no effect of trial: χ2 (1) = 3.41, *p* = .06 and no effect of group (Edinburgh or Leipzig): χ2 (1) = 0.32, *p* = .57.

Experiment 3A – Barrier Task (Transparent window): A binomial GLMM [pass side ~ barrier side + group + (1|subject)] revealed a significant effect of barrier side on passing location: χ2 (1) = 6.95, *p* = .008, OR = 3.52; and no effect of group (Edinburgh or Leipzig): χ2 (1) = 0.12, *p* = .73. When chimpanzees were required to make a binary choice between passing to an obstructed vs an unobstructed side, they passed to the unobstructed side more.

Experiment 3B – Barrier Task (Mesh window): Chimpanzees passed the stick further towards the unobstructed hand. An LMM [pass location ~ barrier side + group + (1|subject)] showed a significant effect of barrier side on pass location: χ2 (1) = 40.97, *p* < .001, *d* = 1.15. I found no effect of group (Edinburgh or Leipzig): χ2 (1) = 1.13, *p* = .29. It is important to note that subjects participated in Experiment 3B after participating in Experiment 4A. In Experiment 4A, they were exposed to an opaque box, and if they passed the stick into the opaque box instead of passing it to the experimenter's open hand, they did not receive a reward. It is therefore possible that the subjects learned that passing to the barrier side was not rewarded.

I also assessed whether the side of the barrier affected the side that subjects passed the tool in Experiment 3B [binomial GLMM: pass side ~ barrier side + group + (1|subject)] and found a significant effect of barrier side: χ2 (1) = 21.88, *p* < .001, OR = 1.97, and a significant effect of group: χ2 (1) = 5.18, *p* = .02. Overall, the side that the subjects passed the stick was affected by the location of the barrier obstructing the experimenter’s actions: chimpanzees passed to the free side.

Experiment 4A – Box Task (Opaque box): A binomial GLM (pass side ~ box side + group) showed a significant effect of the side of the box on the side subjects passed the stick: χ2 (1) = 130.45, *p* < .001, OR = 14.01; and a significant effect of group: χ2 (1) = 4.14, *p* = .04. Subjects' passing side was affected by the location of the opaque box, and they were more likely to pass to the open side.

Experiment 4B – Box Task (Transparent box): A binomial GLMM [pass side ~ box side + group + (1|Subject)] showed a significant effect of the side of the box on the side subjects passed the stick: χ2 (1) = 43.66, *p* < .001, OR = 3.04; and no effect of group: χ2 (1) = 2.03, *p* = .15. Subjects' passing side was affected by the location of the transparent box, and they were more likely to pass to the open side.

In both cases with an opaque and transparent obstruction to the experimenter's action, subjects more frequently passed the stick to a location from which the experimenter could readily grasp it than to the blocked location. The larger effect size in Experiment 4A (opaque box) compared to Experiment 4B (transparent box) suggests that the two types of obstruction elicited different magnitudes of effect on passing behaviour: when the experimenter's actions were blocked with the opaque box, chimpanzees passed to the free side more so than with the transparent box.

Vertical passing location

I found no difference in vertical passing locations in any experiments for which this analysis was possible, that is, experiments with the mesh window (Experiment 1: χ2 (2) = 0.32, *p* = .85; Experiment 2: χ2 (1) = .59, *p* = .44; Experiment 3B: χ2 (1) = 1.91, *p* = .17).

For Experiment 3B, I looked at whether, when passing to the side which the barrier was on, chimpanzees passed higher to account for the obstruction to my actions (note that this was only possible for 7 of the 12 subjects as 5 subjects only passed to either the free side or barrier side). A Gamma GLMM [vertical passing location ~ barrier side pass + group + (1|subject)] showed no effect of whether the subject was passing to the barrier side or free side on vertical pass locations: χ2 (1) = 0.44, *p* = .51; and no effect of group (Edinburgh or Leipzig): χ2 (1) = 0.30, *p* = .58.

Discussion

Humans have a strong drive towards cooperating (Tomasello, 2014), and this can be seen when humans choose to engage in collaborative actions to achieve a goal over choosing to engage in solo action. The extent to which chimpanzees engage collaborative mechanisms, however, is debated. The present series of experiments investigated chimpanzee potential to attend to, represent, and plan joint actions: collaborative cognitive processes that are often thought of as a special part of human cognition. The results from this handover task indicate that chimpanzees do have the capacity to attend to and represent the possible actions of a co-actor and alter their behaviour to adapt to that collaborative partner, demonstrating a signature of human joint action.

Experiment 1 showed that chimpanzees shifted their passing location towards the experimenter's hand in a joint handover-to-retrieve task, possibly indicating action accommodation. However, a bottom-up attentional explanation of the results is also possible here. Subjects may have attended to the experimenter’s hand as the most salient feature in the environment and thus passed to that location. The following experiments were designed to be more robust tests of chimpanzees’ potential to account for and incorporate a task partner’s actions into their own action plans. Experiment 2 tested whether the chimpanzees would account for the action capabilities of the experimenter. The experimenter could only grasp the stick with one hand as their other hand was occupied. The results indicate that the chimpanzees did, indeed, account for the experimenter's action capabilities, demonstrated by a shift in passing location towards the experimenter’s hand that could be used to grasp the stick. Even with a binary choice that required greater movement between the choice of an unobstructed or obstructed side (Experiment 3A), action accommodation was observed. When chimpanzees could choose any passing location (Experiment 3B), a shift towards the experimenter’s unobstructed hand was also observed along the horizontal axis. Overall, the data demonstrate observable behavioural changes consistent with the notion that joint action efficiency is attended to or represented. Lastly, when human action was not possible at one location (Experiments 4A & B), a clear preference to pass to the side where there was the possibility of action was observed.

Although the data are consistent with chimpanzees’ possessing a cognitive system that understands the action demands of a co-agent and represents the actions required to meet a joint goal, the level of shared intention required is an open question. Chimpanzees may generate motor commands based on an internal model of the joint action without explicitly representing the notion of ‘working together’. The co-agent could simply be a ‘social tool’, and these findings do not necessarily indicate shared intentionality to work together.

At a minimal level, an attentional explanation may also be possible for experiments beyond Experiment 1. If chimpanzees represent the expected action of their co-actor, their attention could be directed towards the hand the co-agent would preferentially use, and their movements would then be shifted towards that hand as a by-product of attention. Indeed, in humans, the hands tend to follow the eyes: what happens within the ocular motor system will directly influence what happens with the hands (Bekkering et al., 1995). Given that human eye movements are proactive and predictive when engaged in a motor task (Flanagan & Johansson, 2003) and that the eye and hand motor systems are closely entwined, attention can then have an unintentional influence on the trajectory of the executed action (Constable et al., 2017). In this sense, the representation and observed behaviour need not be as ‘intentionally social’ as they seem, but explained by lower-level processes that manifest as socially optimal behaviour.

It may be more cognitively demanding to perceive a transparent object as an obstruction to action for the co-agent compared to a more salient, opaque box. Thus, if a transparent barrier is not as salient or noticeable as something opaque, then it follows that the extra effort required for the co-agent to overcome the barrier would not be integrated into a sequential action plan as readily. Indeed, chimpanzees accommodated the action of the experimenter more when the obstruction was opaque than transparent in Experiment 4, although action accommodation occurred under both conditions.

Taken together, the data from all experiments indicate that chimpanzees can represent a co-agent's action capabilities and incorporate them into a joint action representation. Nevertheless, the tendency to engage in such processes may differ between humans and chimpanzees. In the present series of studies, chimpanzees received a food reward for engaging in the task and may have been motivated to accommodate the experimenter’s actions to access this reward in the most efficient manner. Whilst it may be the case that chimpanzees have the cognitive capacity for this aspect of joint action, there may be some contexts in which they lack the motivation to act in an accommodating manner. For example, humans are motivated to assist without reward, whereas chimpanzees may be less so. This possible difference in motivation is consistent with the finding that, unlike humans, chimpanzees prefer to work alone than with a partner unless rewarded more for collaborating (Rekers et al., 2011). A drive towards co-efficiency may be a strong enough attractor or reward to influence action execution in joint tasks for chimpanzees, in the present case, because the effort to adapt is relatively minor.

It is important to note that learning is a critical component of the development and refinement of internal models of action. Through experience, an agent updates their internal models for action relative to the consequences of their experiences. This learning then assists the agent to select the most appropriate action within their existing representational framework. This idea links in well with associative learning which is a mechanism that is commonly raised within the comparative literature (Heyes, 2012), and indeed theory pertaining to human joint action processes (Heyes, 2016). In the present work, chimpanzees' prior history of observing an open hand grasp an object may activate a motor plan to pass an object to that hand. That is, the chimpanzee has refined their internal models for action combined with the consequences of that action within a joint context over time. This experience then assists in activating a motor plan that is consistent with more efficient joint action. In this sense, the present results may not generalize readily to wild chimpanzees that have little exposure to humans. Nevertheless, the results demonstrate that the cognitive basis to engage in such joint action is present in chimpanzees.

The present work investigated a handover task where the recipient was always a human, and social dynamics did not differ greatly. Yet, social dynamics can strongly influence how humans engage in joint action. For example, status differences play a role in how joint action phenomena are observed, such as gaze cuing (Dalmaso et al., 2011), co-representation (Aquino et al., 2015), and joint action planning (Boukarras et al., 2021). Further, in a similar handover task to the one presented, gender differences within a human dyad influenced the observation of action accommodation (Dötsch & Schubö, 2015). Specifically, males did not demonstrate a propensity to accommodate a female partner's action, but they did accommodate a male partner's action. Females accommodated the action of both male and female partners. Given that social hierarchy and sex differences are a salient feature of both the human and chimpanzee social landscape, future work could investigate the extent of action accommodation between chimpanzee pairs and investigate action accommodation as a function of status differences. It may be that the results would differ in alternative social dyads with differing social dynamics, and caution should be taken when generalising results from interactions between zoo-housed chimpanzees and humans they interact with frequently.

It should be noted that the frequency of tool handovers varies between experiments with zoo-housed chimpanzees. Whilst in some cases, chimpanzees readily pass tools to a conspecific requesting help (Yamamoto et al., 2012), in other cases, this helping behaviour is rare (Nolte & Call, 2021). Nolte & Call (2021) suggest that differences between studies may be due to differences in experimental set-ups. Specifically, when chimpanzees are only presented with one task, namely handing over a tool, they seemingly do so readily. In contrast, when they have an apparatus in front of them to engage with, they are less inclined to pass a tool. Furthermore, training chimpanzees to work on the apparatus alone may have led chimpanzees in Nolte & Call (2021) to conceive their task as non-cooperative. In the current study, all experiences with the experimental set-up involved working together with an experimenter, and the only way to engage with the task was to pass the tool. Critically, our task looked at *how* the tool was passed, and not *if* it was passed, so issues of motivation and distraction should not have influenced this study in the same way. Interestingly, bonobos were shown to pass tools to conspecifics in the Nolte & Call (2021) study, suggesting that in some cases they may be more motivated to cooperate than chimpanzees, or at least that they are more receptive to a partner's requests for help. This is further supported by findings with two groups of bonobos showing more cooperative success than chimpanzees when a food reward could be monopolised (Hare et al., 2007; Nolte et al., 2023). Given this species difference, it may be that bonobos would perform differently to chimpanzees in the current task and may be even more willing to facilitate a partner's action ease, such as in cases where they do not directly benefit from efficient action as was the case here.

A limitation of this study is the lack of a non-social control condition. It cannot be concluded from this study whether this accommodation behaviour is a facet of chimpanzee social cognition, or a demonstration of choosing an efficient course of action to complete a goal. The chimpanzee's goal in this task is to transport the tool to the experimenter's hand, but their avoidance of obstacles when completing this goal could also be present when transporting a tool to other locations. For example, if the task had been to place the tool onto a tray on the experimenter's side of the window, their passing location may have also shifted away from barriers and obstructions. In humans, slight differences are seen in motor sequences to pass an object to another person compared to placing the object somewhere individually (Becchio et al., 2008). Although these results suggest that chimpanzee's internal action models are influenced by features of their environment, without the appropriate controls in place, caution should be taken before determining that this behaviour is social or that chimpanzees use this ability in other cooperation contexts. Nevertheless, these results demonstrate that in some cases, social stimuli (in this case, the experimenter) can be integrated into chimpanzee's action models. This task could be expanded to include more fine-tuned action accommodation such as altering the orientation with which a tool is passed based on what the receiver will use it for (Gonzalez et al., 2011). Future research into chimpanzee social cognition should implement non-social controls to tease apart which aspects of social behaviour are domain-general, and which may be specifically recruited for social interaction.

Our results provide evidence that chimpanzees, at least when they stand to gain something for themselves, may represent a co-agent's actions and that representation can be observed in their own action execution during social coordination. Specifically, chimpanzees flexibly shifted their passing location in response to features of the joint action environment during a handover task. This indicates that chimpanzees can engage similar joint action mechanisms to humans, contributing to the foundational and evolutionary understanding of the cognitive underpinnings of social coordination.

Chapter 3: Chimpanzee action learning in a cooperative task[3]

Summary

When working with a partner, humans often represent both their own actions and the actions of their partner. Additionally, humans may have a sense of shared obligation, or joint commitment, to complete tasks. This study investigates action learning during a co-operative task between chimpanzees and a human experimenter. Two distinct actions were required to achieve the goal of food retrieval; in a co-operative condition the first action (flipping a see-saw style apparatus) was completed by the experimenter, and in a non-social control condition, the same first action was caused by an object falling. In both conditions, chimpanzee subjects completed the second action (pulling a piece of paper to access a food reward). After experiencing one of these two learning conditions, subjects were given a test phase in which it was now their task to complete both actions. I looked at the overall number of successes; that is, how many times subjects successfully performed both actions, the number of incorrect responses; that is, completing the second action (paper pull) without having completed the first (flipping the see-saw), and the latency to perform both actions. If during the cooperative learning context, chimpanzees represented their partner's actions, they may more readily perform that action themselves in the test phase. Additionally, I looked at the rate of leaving the testing area during the test phase, and the latency to leave. If the cooperative condition promoted a sense of joint commitment, chimpanzees may wait later before leaving the task set-up as they have a greater expectation of the experimenter's action. I found no difference in overall rate of completing

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[3] This project was a collaboration with Elizabeth Warren. Parts of the methodology and results have been omitted here and included only in Elizabeth Warren's thesis. Data was collected by Elizabeth Warren.

the flipping action, but qualitative differences in technique between conditions is discussed. No evidence of a different sense of joint commitment was found between conditions. These findings indicate possible action co-representation during co-ordination in chimpanzees, although further control conditions are needed.

Introduction

A key aspect of many coordination definitions is the requirement that an agent considers not just their own actions, but the actions of their task partner too (for example, Michael et al., 2020). Often in social co-ordination studies with primates, it can be challenging to infer what subjects are representing about the task. Subjects could each be focused only on their own role in achieving the goal and successfully work together, but somewhat separately (Noë, 2006); they could achieve the goal together without any sense of what the other did. Many would argue that this sort of solution does not reach the criterion for coordination (Michael et al., 2020; Knoblich et al., 2011: "planned coordination"). The level of representation that primates engage during coordinative tasks is an ongoing conversation in the field of Comparative Psychology (Duguid & Melis, 2020).

When engaging in a co-ordination task, there may be an understanding of the shared obligation to complete the goal, referred to as joint commitment (Clark, 2006). This is demonstrated in humans' day-to-day social lives both in our behaviour, such as fulfilling commitments we make to one another (for example, turning up when we offer to help a friend move house, or resuming a conversation after an interruption), and in our reactions to breakdowns in such commitments (for example, feeling annoyed if our friend does not show up to help with a house move after agreeing to, or they walk away mid-conversation) (Michael et al., 2016; Heesen et al., 2021). Michael et al. (2016) define a minimal structure in which a sense of commitment can arise as an agent having a goal which requires the external contribution that a second agent has agreed to make. This sense of joint commitment is evident in young children (3 years), who resist the temptation to leave a shared task for a bribe when the joint aspect of the task is made explicit. Joint commitment in slightly older children (5 years) is seen without the need for explicitly noting that the task is shared, demonstrating an understanding of the interdependence of their actions and a commitment to their shared goal (Kachel & Tomasello, 2019). Even younger children (18-24 months) attempt to re-engage a partner in a social game when they disengage, which could be interpreted as a response to a break of a joint commitment (Warneken et al., 2006). Warneken and colleages (2006) did not find the same results with chimpanzees in the same task, however, but later research has shown that chimpanzees are sensitive to some co-ordination breakdowns (Voinov et al., 2020). There is some recent evidence for certain joint commitment processes in bonobos, whereby there is seemingly communication before disengaging from a joint task, and more task re-engagement after interruptions to a joint activity than a solo activity (Heesen et al., 2020), possibly suggesting a sense of joint commitment. It cannot be ruled out, however, that the apes in this study were more likely to reengage a social task as it was more rewarding (Tomasello, 2022).

There is evidence that chimpanzees can learn actions by observation; they demonstrate some social learning abilities. Social learning has been inferred from the behaviour of wild populations of chimpanzees, for example, nut-cracking, which is thought to be rather complex, has not been re-invented by captive unenculturated apes and perhaps requires learning from social models (Koops et al., 2022). Social learning has also been demonstrated in experimental contexts with captive groups of chimpanzees. For example, in Whiten et al.'s, (1996) work, for some individuals, the type of solution for a task was influenced by the specific demonstration observed. Additionally, chimpanzees appear to be sensitive to the action capabilities of an experimenter and tailor their responses to whether the experimenter is unwilling or unable to give them food, at least in situations in which the experimenter acts on the food (Call et al., 2004). This further demonstrates some ability to reason about another's actions. While there is some disagreement over whether or not behaviour can be socially learned in non-humans (Whiten, 2022; Tennie, 2023), it has been reported across several species (bumblebees: Smolla et al., 2016; bearded dragons: Kis et al., 2015; and many more species, largely with a focus on corvids, primates, and cetaceans: Allen, 2019). The social transmission of behaviour in chimpanzees could be evidence that, in some contexts, chimpanzees possess a system for representing (and hence learning from and sometimes mimicking) other's actions. Whether or not this is a faculty also co-opted for joint action tasks remains to be answered.

A distinction has been made between imitation and emulation. Whereas imitation refers to reproducing a behaviour by copying the action components, emulation refers to reproducing a behavioural outcome but not necessarily using the same exact means (Boesch & Tomasello, 1998). Opinions and experimental results differ regarding whether or not chimpanzees imitate or emulate actions (Tennie et al., 2006). While some suggest that chimpanzees copy behavioural methods (for example, Whiten, 1996, 1998), others find evidence that the type of demonstration observed does not affect the methods with which chimpanzees solve a task – in contrast to human children (Nagell et al., 1993). Tennie et al., (2006), building upon Call and Carpenter's (2002) work, suggest that actions could be learnt from the following: end-states, object affordances, and object movements. These strategies would be considered emulation (also referred to as 'results copying') rather than imitation (also referred to as 'action copying'). As imitation requires some representation of the social model’s actions, it follows that this may be used this to facilitate co-ordination, and so could be harnessed as a method to study the action representations involved in joint tasks. Imitation and joint action are connected phenomena and research on the two topics share focuses such as mapping another’s actions onto one’s own motor system (to learn from, or to make predictions about actions), and working jointly may aid information transmission (McEllin et al., 2018).

Here, I present a study looking at action learning during a cooperative task. Chimpanzees engaged in a task with two-actions; the first action was flipping a see-saw style apparatus so that a grape would roll onto a piece of paper, the second action was pulling the piece of paper to retrieve the grape. In the co-operative condition, the first action was performed by a human experimenter. In a non-social control condition, the first action was achieved by an object falling onto the apparatus. Two distinct actions were chosen for this task so that during the training, the only action that subjects were executing was the paper pull, while the other (see-saw flipping) was only observed. After experiencing this task with either the experimenter or object, I introduced a test phase with a co-ordination breakdown: either the experimenter no longer performed the action (cooperative condition), or the object did not fall onto the apparatus (object condition). Further, during this stage, subjects were given access to the see-saw apparatus which had been previously blocked. In both conditions, the experimenter was always present during training and test phases, as infant studies have shown that social model presence influences the likelihood to imitate an action (Király, 2009). In the non-social object condition, an object clearly falls onto the apparatus to cause the action, as alternative ‘ghost’ controls with no clear reason for inanimate objects moving may be more difficult to learn from than causal contingencies (Call, 2006).

Previously, in a collaborative task with two complimentary roles, Fletcher et al. (2012) reversed the roles of two chimpanzee collaborators and assessed whether the experience as a collaborator helped them solve the task faster. They compared the speed of solving Role B of the task between the first chimpanzee and the second, who had initially taken on Role A. The authors found that six out of seven pairs successfully swapped roles, and the second chimpanzee required 50% less time on average than the first to solve the task, but this did not reach statistical significance in this sample and the authors concluded that chimpanzees had not represented both actions during the initial collaboration. Tomasello (2022), however, points out that the actions required in this task were fairly complex, including grapes rolling down ramps and opening a spring-loaded door over three levels of the apparatus. This may have made vicarious action learning particularly challenging with this apparatus. Given the small difference that Fletcher et al. (2012) found between subjects with a complex apparatus, it is plausible that with a simpler set-up, action learning differences may be clearer.

I compare the ability of subjects in each condition to perform the first action in this test phase, having only watched either an experimenter or object cause the action. Crucially, the outcomes in both conditions were identical (the grape rolls down the see-saw onto the paper) and only the means and causes were different (social and non-social). I hypothesise that, if during the cooperative training chimpanzees represented their partner's actions, they should more readily perform the first action in the test phase than those chimpanzees who only saw the first action occur via an object falling. Subjects will still be able to pull the paper during this test phase regardless of whether or not they have performed the first action; pulling the paper before the see-saw has been flipped constitutes an incorrect trial. Even if there are no difference in correct responses between conditions, latencies to respond may still differ, possibly indicating that chimpanzees in the cooperative conditions expect their partner to respond. I hypothesise that subjects in the cooperative condition will wait longer before pulling the paper in incorrect trials, wait longer before leaving, and leave less often as they will have a greater expectation of the first action occurring due to the joint commitment formed between subject and experimenter.

Methods

Subjects

Ten chimpanzees participated in this study (4 females and 6 males, mean age 29.8 years [SD = 12.5, range = 5.2 – 44.5] at the beginning of data collection). Five chimpanzees were randomly assigned to the co-operation condition (2 females and 3 males, mean age 28 years [SD = 14.7, range = 5.2 – 42.8]) and five to the object condition (2 females and 3 males, mean age 31.6 years [SD = 11.3, range = 20.6 – 44.5]), shown in Table 2.

Subjects were housed at the Budongo Research Unit (BRU) in Edinburgh Zoo, Scotland. Housing details for Edinburgh Zoo can be found in Chapter 2.

Table 2: Subject demographic information.

Name	**Condition**	**Sex**	**Age (years)**
Velu	Co-operation	M	5.2
Qafzeh	Co-operation	M	27.4
Frek	Co-operation	M	25.8
Eva	Co-operation	F	38.8
Lucy	Co-operation	F	42.8
David	Object	M	44.5
Louis	Object	M	43.1
Liberius	Object	M	20.6
Kilimi	Object	F	26.5
Edith	Object	F	23.4

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 was also approved by the BRU committee (consisting of the Zoo Research Liaison Officer, the Scientific Director, and the Research Coordinator) as well as by the School of Psychology and Neuroscience Research Ethics Committee at the University of St Andrews.

Apparatus

Chimpanzees sat on one side of a mesh window, and I faced them on the other side of the mesh. On my side was a table with an additional sliding table placed on top, upon which sat the ‘see-saw’ apparatus (Figure 6). The ‘see-saw’ was a wooden apparatus with a 45cm x 25cm piece of wood on a 6.5cm fulcrum, so that each end of the wood could be tilted up or down, akin to a see-saw. The side that was resting on the table (low side) sat at 3cm tall, the height in the air (the high side) sat at 9cm tall. There was a 7cm wide groove in the see-saw (10 cm and 28cm from left and right edges from my perspective, respectively), inside which I placed a strip of paper to be pulled by subjects. The ‘see-saw’ was slightly weighted on one side (experimenter’s right) to avoid being accidentally flipped into the correct position. There were also wooden blocks (8cm x 2cm x 2 cm) in front of the see-saw to stop grapes from rolling away once they had been successfully retrieved, and a wooden barrier on one end of the see-saw to keep the grape in place at the start of trials. In the object condition, an additional lever (18cm x 2cm x 2cm, with a wooden base of 8cm x 4cm) was used to flip the see-saw. This lever was made from a combination of wood and a metal doorstopper and was attached to a piece of string (approximately 110cm) to be covertly operated by me. Testing took place in an alcove of the testing room with two testing windows perpendicular to one another, so that during the test phase the window to my left could be opened allowing subjects access to flip the see-saw (Figure 7).

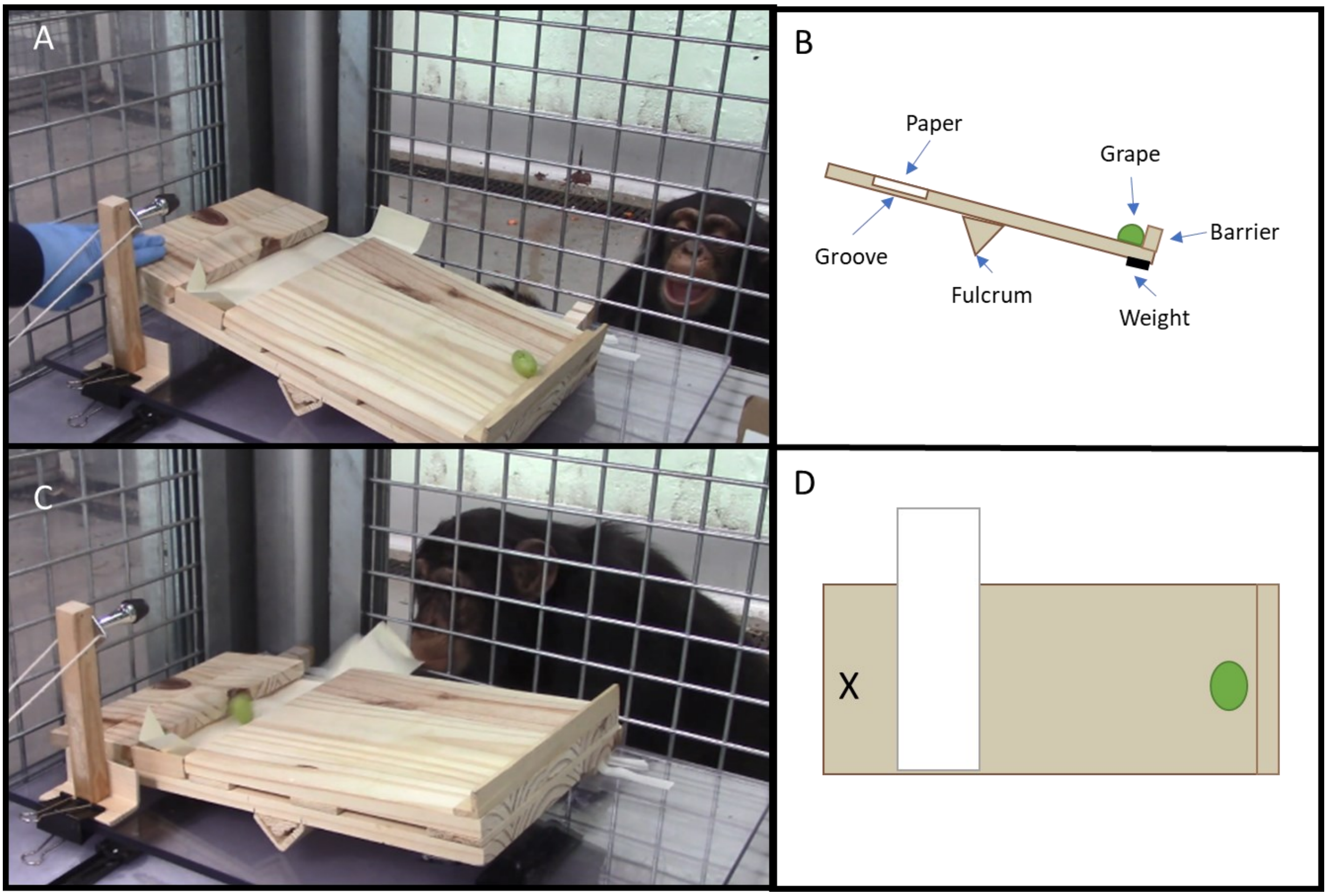

Figure 6: Top left (A): See-saw apparatus in the starting position, about to be flipped by the experimenter. Next to the experimenter's hand is the lever used in the object condition. Top right (B): graphic of see-saw apparatus at the start of a trial, before it has been flipped. Bottom left (C): After the see-saw has been flipped, the subject (male, Velu) is pulling the paper to retrieve the grape. Bottom right (D): overhead view of the see-saw apparatus at the start of a trial, before it has been flipped. X indicates the approximate location of the experimenter's hand or object (lever) when flipping the apparatus.

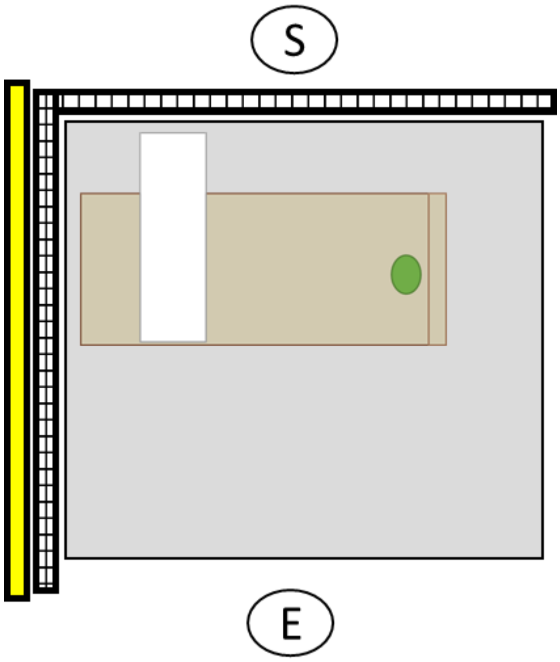

Figure 7: Overhead view of testing area. Circle with E indicates experimenter, circle with S indicates subject. The grey square indicates the table upon which the see-saw apparatus was placed. During the pre-tests, learning phase, and communication phase, the window to the left of the experimenter was blocked with a polycarbonate panel (highlighted yellow, but note this was in reality transparent). During the test phase, this highlighted panel was removed, and the mesh window was open, with the apparatus accessible by subjects from the side.

Procedure [4]

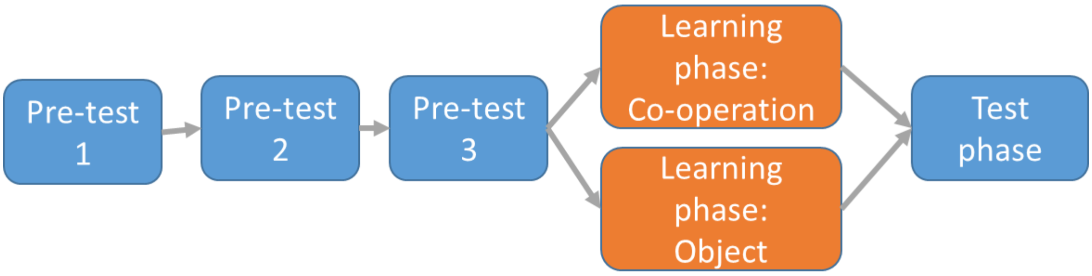

Figure 8: Overview of experimental phases. Blue shapes indicate phases which were identical between conditions, orange shapes indicate phases which were dependent on condition.

In both conditions, all subjects experienced all following stages of the experiment, and only their learning phase differed (see Figure 8).

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[4] Data collection was interrupted multiple times due to COVID-19 lockdowns and related research disruptions. Details of deviations from the protocol in relation to these disruptions can be found in Appendix A. A general rule was applied of ensuring each subject had at least 10 learning trials directly before moving to the test phase.

Pre-test 1: The first pre-test tested whether subjects understood that they must pull the paper with a grape on it. I placed two strips of paper onto the testing table in front of the subject, one with a grape on it, and the other with a grape next to it. The strips of paper were either close together, or far apart, presented in blocks of 6 trials with the block order randomised between subjects. I pseudo-randomised the side of the baited and non-baited strips of paper such that no more than 3 trials in a row had the baited paper on the same side. For the non-baited paper, I always placed the grape on the outer edge. That is, when the non-baited paper appeared on the left, I placed the grape to the left of the paper, and when it appeared on the right, I placed the grape to the right of the paper. All subjects received one session of 12 trials of this pre-test.

Pre-test 2: The second pre-test tested whether subjects could inhibit pulling the paper until it had a grape on it. I placed a single strip of paper on the testing table in front of the subject and waited either 0, 3, or 5 seconds before placing a grape onto the paper. I pseudo-randomised the waiting time between trials such that no more than 3 of the same trial type appeared in a row, and no session (block of 12 trials) began with a 5 second trial. Each session consisted of 12 trials, with 8 of these being probe trials (trials with a wait time of 3 or 5 seconds). The pass criterion for this pre-test was two consecutive sessions with at least 13/16 probe trials correct. That is, subjects had to wait for the grape to be placed on the paper before pulling the paper in at least 13/16 trials with a 3 or 5 second wait time. Subjects Eva, Louis, and Edith passed in 3 sessions; subjects David and Kilimi passed in 5 sessions; subjects Lucy, Liberius, Velu, and Qafzeh passed in 7 sessions; and subject Frek passed in 11 sessions.

Pre-test 3: The final pre-test tested whether subjects could wait for the grape to roll onto the paper before pulling it. Here, I placed the see-saw apparatus on the testing table in front of the subject with a piece of paper on it, as in the learning and test phases. Here, however, I already placed the see-saw in a downward position, so no flip was required. At the start of each trial, I placed a grape on the high end of the see-saw so it would roll down onto the paper. Subjects were required to pull the paper off the see-saw in 10/12 trials. All subjects received a total of 24 trials of this pre-test.

Learning phase: Subjects received 100 learning trials each. From the experimenters' perspective, the see-saw always started with the right side down and left side up. With the see-saw apparatus occluded, I placed a grape on the right, downward side, then pushed the sliding table towards the subject and removed the cardboard occluder. The see-saw was always at an out-of-reach distance, and only the strip of paper could be reached by subjects. In the co-operation condition, I then flipped the see-saw by placing my hand on the left (from my perspective), upward side, and moving it to a downward position so that the grape would roll onto the strip of paper. In the object condition, the lever 'fell' onto the see-saw (the string it was attached to was loosened by me, out of sight, so that it would drop and hit the see-saw) and moved the left side down so that the grape would roll onto the strip of paper. Subjects then pulled the strip of paper towards themselves to retrieve the grape. If subjects were interrupted by a group mate, trials were re-started.

Test phase: Subjects received 12 test trials each, which were identical between the two conditions. During the test phase, a window to my left which was previously blocked was now open, allowing subjects access to the apparatus from that side (see Figure 7). I occluded, baited, and pushed the see-saw apparatus towards the subject as in the learning phase. Now, however, when I removed the occluder, the see-saw was not flipped by me nor by the object. Subjects were given 60 seconds to flip the see-saw themselves from the newly opened window. If they did not succeed in this time, I ended the trial by moving the see-saw away from the subject, and started the next trial. If subjects incorrectly pulled the paper without flipping the see-saw beforehand, that is, the grape was not on the paper, they were given 30 seconds, or until the end of their 60 second trial (whichever was shortest) to evaluate the apparatus, then I ended the trial.

If subjects left the testing area and did not return within their remaining trial, or if another subject arrived at the testing window to participate, I ended the trial. If subjects were interrupted by a group mate, trials were re-started.

An example video can be found for this experiment via the following link: https://osf.io/pjgnh/?view_only=3b17b2f191e045cd871f045bc48ca331

Coding and data analysis

I coded all occurrences and latencies of flipping, pulling, and leaving from video recordings using the Behavioral Observation Research Interactive Software (BORIS), (Friard & Gamba, 2016). Analyses, visualisations, and model formation followed the same procedure as laid out in Chapter 2. I coded a 'flip type' variable by categorising how subjects flipped the see-saw, characterised as either 'proper flips' or 'alternative flips' (see coding scheme in Table 3).

A research assistant separately coded a subset of the data for reliability analysis of flipping and pulling variables (15% of trials across subjects). I evaluated consistency in coding using Cohen's κ for judgements on binary variables, and ICC for latencies. Excellent reliability was found for the occurrence of a flip (κ = 1, *p* < .001), type of flip; proper or alternative, (κ = 1, *p* < .001), occurrence of a complete pull (κ = 1, *p* < .001), latency to flip (ICC = 0.994, *p* < .001), and latency to pull (ICC = 1, *p* < .001).

Another experimenter separately coded 'leaves' in a subset of the data for reliability analysis (33% of trials across subjects). I evaluated consistency in coding for frequency of leaves, and latencies of leaves in those trials for which this was possible (trials in which both coders had coded a leave). I found good reliability for the frequency of leaves (ICC = 0.81, $p < .001$) and excellent reliability for leave latencies (N = 14, ICC = 0.96, $p < .001$).

Coding scheme

Table 3: Ethogram used for video coding.

Behaviour code	Definition
Trial start	Timestamp of point when the experimenter starts to lift the occluder
Trial end	Timestamp of point when the experimenter starts to pull the sliding table backward
Complete pull	Timestamp of point when paper is pulled by the subject completely clear of seesaw
Trial success proper	Timestamp of flip with hands by the subject, before/without a complete pull
Trial success alternative	Timestamp of flip by alternative means by the subject, before/without a complete pull
Leave	Timestamp of the subject leaving the testing area (defined as between the front panel and the back wall. And one arm's reach away from the side panel).

Table 4: Overview of alternative flip types.

Subject	Alternative flip type	Technique	Frequency
David	Object	Stick	1
Kilimi	Object	Paper lever	3
Edith	Object	Paper lever	5
Eva	Co-operative	Paper lever	1

Results

Flipping

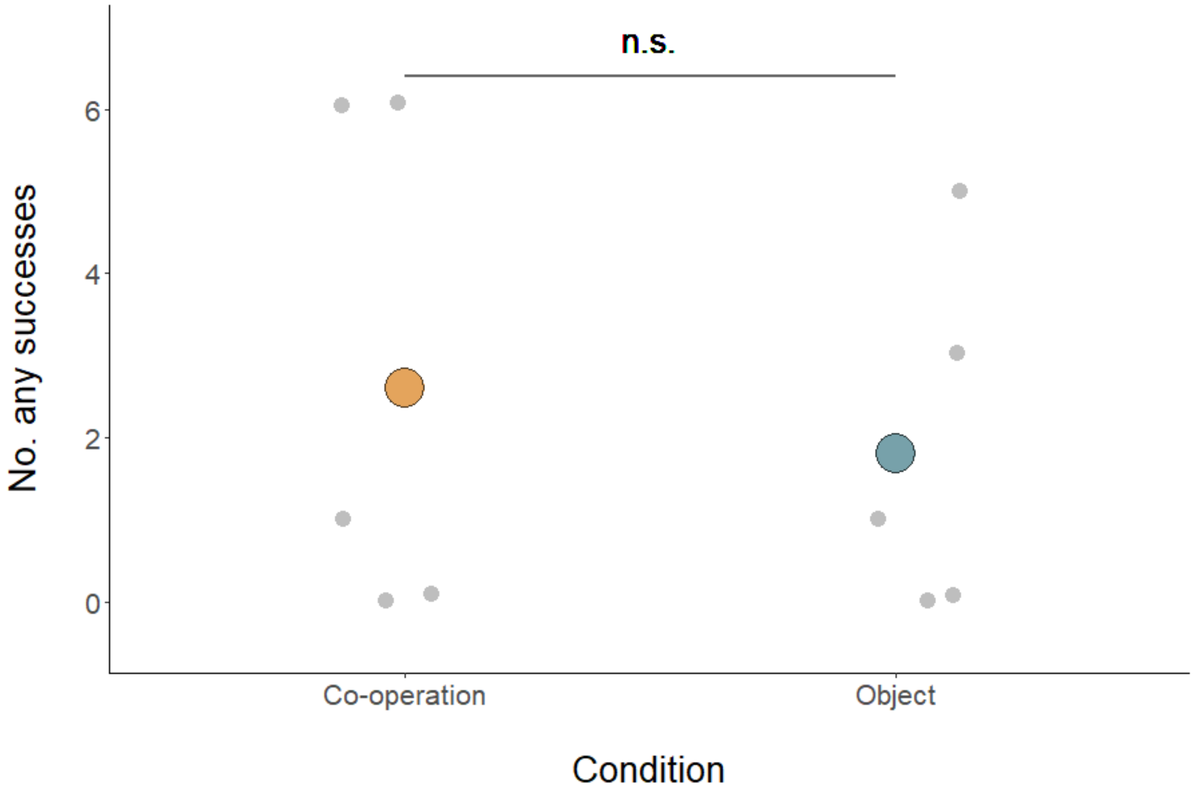

Figure 9: Number of flips by any means across 12 test trials between co-operation and object conditions.

Flipping rate: A binomial GLMM [Flip ~ Condition + Trial + (1|Subject) + (0 + Trial|Subject)] showed no effect of condition on likelihood to flip across trials in the test phase (Condition: χ2 (1) = 0.23, *p* = .63, OR = 0.33); the likelihood of a subject successfully flipping the see-saw on any given trial in the test phase was not affected by whether their learning condition was co-operative or with an object (Figure 9).

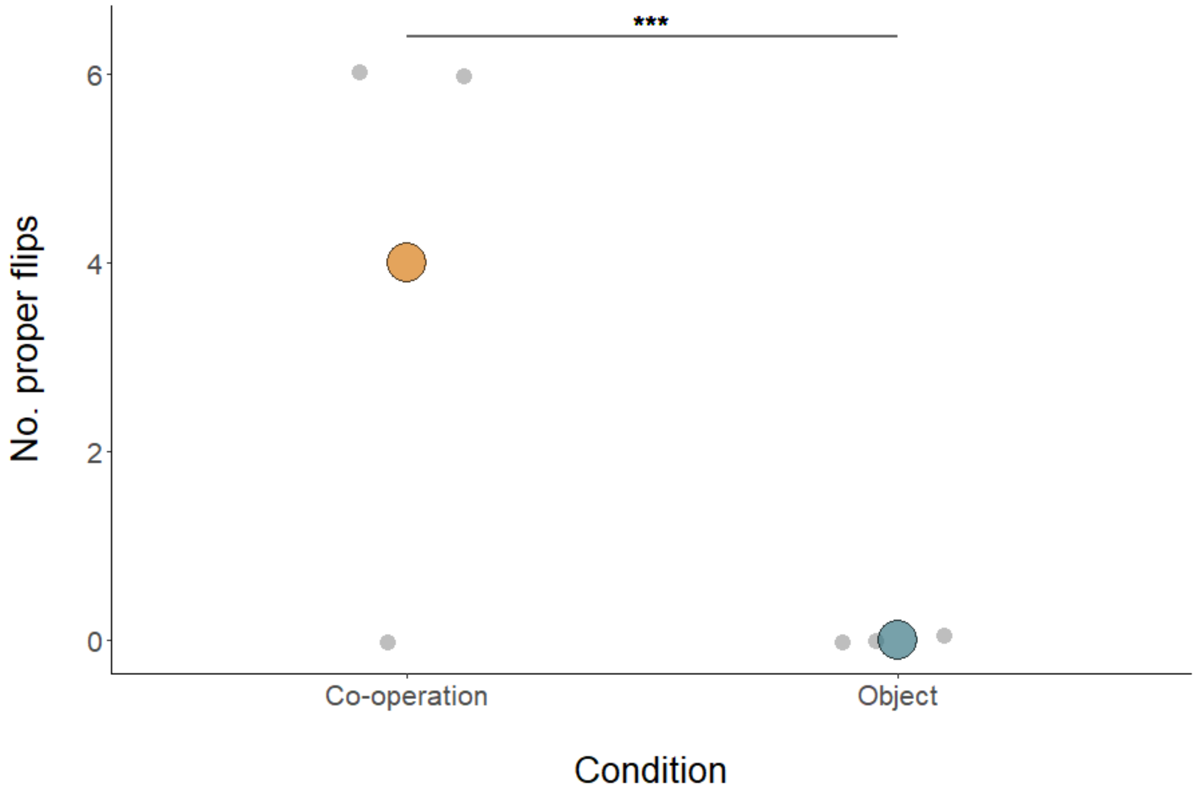

Figure 10: Number of proper flips across 12 test trials between co-operation and object conditions. Graph includes all flips from both conditions, and Y-axis depicts a count of how many of those flips were counted as ‘proper’ rather than ‘alternative’.

I conducted a second analysis including only those subjects who had flipped the see-saw to assess the effect of condition on type of flip (proper or alternative). A binomial GLM (Proper flip ~ Condition) showed a significant effect of condition on flip type; those subjects whose learning condition was cooperative were more likely to use a ‘proper flip’ and those whose learning condition was with an object were more likely to use an ‘alternative flip’ (Condition: $\chi 2$ (1) = 23.27, $p < .001$, OR < .001), see Figure 10.

An exploratory binomial GLMM [Flip ~ Condition*Trial + (1|Subject) + (0 + Trial|Subject)] looking only at those subjects who flipped revealed an interaction effect of condition and trial on flips; subjects in the cooperative learning condition flipped more consistently than those in the object condition (Condition*Trial: χ2 (1) = 3.7, *p* = .054, difference in estimated trends = -3.34), see Figure 11. That is, once they had flipped once, subjects in the cooperative learning condition tended to continue flipping, whereas subjects in the object condition either flipped sporadically, only once, or discontinued flipping.

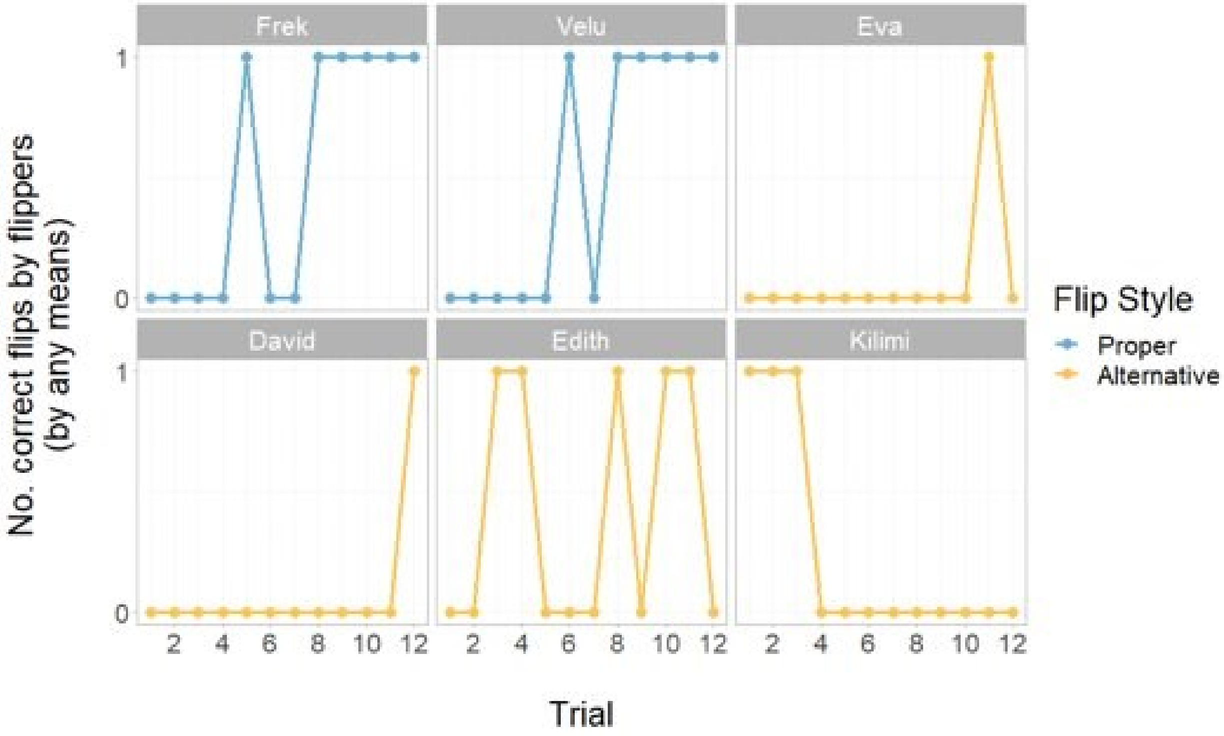

Figure 11: Flipping by any means across trials in the test phase. Subjects in the co-operation condition are shown in the top row, subjects in the object condition are shown in the bottom row. Colour indicates whether the subject's flip style was 'proper' or 'alternative'.

Flipping latency: A Gamma GLMM [(flip latency) ~ Condition + Trial + (1|Subject)] found no effect of condition on latency to flip: χ2 (1) = 0.03, *p* = .86; and no effect of trial: χ2 (1) = 2.81, *p* = .09. The learning condition did not impact the time it took those chimps who flipped in the test phase to do so.

Pulling paper

Pulling rates in incorrect trials: A binomial GLMM looking at pulling the paper only in incorrect trials [Pull ~ Condition + Trial + (1|Subject)] showed no effect of condition: χ2 (1) = 0.31, *p* = .58, OR = 1.39. Subjects did not incorrectly pull the paper before flipping the see-saw apparatus at significantly different rates between the two conditions. The odds ratio, however, revealed that, numerically, subjects in the cooperation condition had less incorrect paper pulls.

Pulling latency in incorrect trials: A Gamma GLMM including only incorrect trials [Pull latency ~ Condition + Trial + (1|Subject) + (0 + Trial|Subject)] showed no effect of condition on latency to pull the paper: χ2 (1) = 0.05, *p* = .82; and no effect of trial: χ2 (1) = 0.02, *p* = .90. Subjects in the object condition did not pull the paper faster or slower than subjects in the cooperation condition.

Leaving

Leaving rate: A binomial GLMM [Leave ~ Condition + Trial + (1|Subject) + (0 + Trial|Subject)] revealed no effect of Condition: χ2 (1) = 0.83, *p* = .36, OR = 1.51; and no effect of Trial: χ2 (1) = 0.34, *p* = .56. Subjects' likelihood of leaving during test phase trials was not affected by their learning condition. Overall, leaving happened relatively infrequently in both groups. The total number of leaves across 5 subjects per group, across 12 test trials, was 18 in the co-operative condition, and 23 in the object condition.

Leaving latency: An LMM including only those trials in which a subject left [Leave latency ~ Condition + Trial + (1|Subject)] showed no effect of condition on latency to leave: χ2 (1) =

0.88, *p* = .35, *d* = -0.36; and no effect of trial: χ2 (1) = 2.83, *p* = .09. Subjects' learning condition did not affect their latency to leave during the test phase.

Discussion

In a partial role-reversal task, subjects did not differ in the overall number of successes based on whether the initial task was cooperative or non-social. However, I found a qualitative difference in the techniques used by subjects differing by condition. Subjects in the cooperative condition used the form used by the experimenter, whereas subjects in the object condition used alternative methods to flip the apparatus, such as using the paper as a lever. Moreover, subjects in the cooperation condition produced flips more consistently, that is, after being performed once, after brief set-backs in performance, flips were performed for the remaining trials. Alternative flips did not show the same level of consistency, and were either performed only once, in a seemingly random distribution across trials, or only in early trials and subsequently discontinued. Flipping style almost perfectly correlated with condition, aside from a single alternative flip from one subject (Eva) in the co-operative condition. The latency to flip, number of incorrect responses, and latency to incorrectly pull the paper did not differ between the two conditions.

Taken together, the differences in flipping styles and consistency suggest that chimpanzees in the cooperative condition and object conditions may have learnt about the apparatus differently. It could be that chimpanzees in the cooperative condition copied more closely the actions of the experimenter whereas chimpanzees in the object condition learnt the affordances of the see-saw, or bootstrapped from the end-state of the apparatus. This interpretation would support the hypothesis that chimpanzees represent their task partner's actions during co-ordination. These results are, however, based on a very small sample as only three chimpanzees from each condition flipped the see-saw, and only two demonstrated ‘proper flips’. Therefore, while this pattern of results is encouraging, further research with larger samples is needed to assess the reliability of these results and rule out other individual differences which could drive the strategies used.

In humans, a joint task elicits a sense of joint commitment, which can create expectations about a partner (Fernández-Castro & Pacherie, 2022). Previous research has shown that great apes wait longer before abandoning a testing station when the experimenter is unable to give them food, suggesting that when there is an expectation of continued interaction or reward, great apes are more willing to wait (Call et al., 2004). In this vein, I hypothesised that chimpanzees would wait longer before leaving, and leave less often, in the test phase if they had experienced the cooperative learning condition than the object condition. I also hypothesized that chimpanzees in the cooperative learning condition would wait longer before making an incorrect response, as they would have a greater expectation that the experimenter would engage in the task. No significant difference was found between conditions, although the pattern of results was in the expected direction, with subjects in the cooperative condition leaving a little less often and a little later than those in the object condition. No significant difference in latency to incorrectly respond was found between conditions, although results were again in the expected direction; chimpanzees in the co-operative condition waited slightly longer to pull the paper. This lack of evidence for chimpanzees’ sense of commitment is in line with previous work showing that chimpanzees do not continue working on a joint task once they receive a food reward, even if their partner is yet to obtain theirs (Greenberg et al., 2010). Overall, subjects left the testing station fairly infrequently. The experimenter was not *unable* to give the subject the reward, nor *unable* to act on the apparatus. Further, subjects in both conditions had lots of experience being fed by experimenters. These factors may have influenced subjects' expectations of how the experimenter would act, more so than my experimental manipulation. The evidence for a sense of joint commitment here may be overshadowed by previous experiences with the experimenter, and thus no clear conclusions can be made about this here.

Another possible interpretation could be made of the findings presented here based on local enhancement (Thorpe, 1956). This refers to attending more closely to certain stimuli or displays, which may have been the case for the cooperative condition here. Research has shown that, like humans, great apes selectively attend to social stimuli, paying particular attention to facial features, but also to the goals of others' actions (Kano & Call, 2017). These biases in attention could be manifest in the results of this study in the following ways: the experimenter's hand could be a more salient display than the falling object; and the cooperative condition containing an agent with a goal could have drawn more attention to the apparatus than the object condition. While social attention more broadly was partially controlled for by having the experimenter present during both conditions, it is possible that more specific areas of the testing environment carried more attentional weight. Further, it is feasible that, particularly in captive ape populations whose lives consist of close contact with humans, that a human hand may hold particular salience. Human hands may have become associated with food or other interesting items which could be held by animal caretakers or researchers. Hands of group-mates could inflict pain, engage in grooming, or communicate through gestures. Secondly, eye-tracking research has shown that great apes look to locations in which they expect an agent to act, but not a non-social object (Kano & Call, 2014; Krupenye et al., 2016).

Furthermore, great apes follow experimenter's gaze (Bräuer et al., 2005). The experimenter only looked at the apparatus during the co-operative condition, in an attempt to minimise their engagement in the object condition. Thus, if chimpanzees followed the experimenter's gaze here, it would follow that they may learn more about the apparatus. In other research employing eye-tracking methods, great apes have shown a better memory for social than non-social events (towers constructed by hands or claws), but no difference in attention to the two displays, suggesting that social information transmission relies on mechanisms beyond attention, which would make the local enhancement explanation of our results unlikely (Howard et al., 2017). It cannot be ruled out, however, that the condition differences mentioned here may have made the cooperative demonstration more interesting to subjects than the object falling, and our results could reflect differences in social attentional processes rather than highlighting social cognition used for co-ordination (Byrne, 2002). Indeed, Zajonc (1965) points out that the presence of other social agents tends to increase activity, termed 'social facilitation'. More research is needed to further tease apart whether this pattern of results reflects intentional consideration of a partner's actions, more automatic attentional processes, or perhaps something in between such as a system for understanding where to direct attention during social co-ordination.

Making a distinction between imitation and emulation is not always straight forward. Byrne (2002) notes that fidelity in behavioural matching is not always necessary when learning actions, rather matching the outcome of an action may be prioritised. Byrne makes a distinction between 'action-level' imitation (copying exact action sequences) and 'program-level' imitation (identifying an underlying plan of behaviour and copying key aspects). Program-level imitation may behaviourally present just as emulation, as in both cases the exact actions of a model may not be perfectly recreated. However, program-level imitation requires identifying which aspects of a behavioural sequence need to be copied, and which could be adapted, allowing for flexibility in the way a goal is achieved. For example, injured apes may imitate behaviour slightly differently to compensate for their own action ability, but could still have learnt about a model's behaviour just as well as an uninjured individual who might imitate with perfect fidelity (Stokes & Byrne, 2001). Great apes have been shown to 'rationally imitate', that is, seeming to consider the logic behind a models' choice of actions (Buttelmann et al., 2007), and so caution should be taken when inferring that behaviour that looks like emulation indicates less task understanding.

A social learning control condition is required to further elucidate which factors drive the differences between the conditions in this study. It is not yet clear whether the 'joint' aspect of the task is important here. As highlighted in the introduction to this chapter, great apes possess a social learning ability, and it could be that the difference in flipping type reflects learning better from a social model than a non-social object. In this case, I was limited by the available sample size and so was unable to conduct further control conditions. If this study were to be replicated and extended, conditions in which the actions are not interdependent, or in which one action is irrelevant to the shared goal, should be included. Additionally, looking only at overall rates of success and discarding the difference in strategy, I saw similar levels of success in both groups. It may be that, as the actions were sequential and the subject faced the experimenter, they were primed to watch the first action, and this might not be something they always do during co-ordination tasks. Future research could look at whether subjects selectively watch a partner's actions, such as positioning them adjacently, and could use live eye-tracking to track their gaze (for example, as in Wolf & Tomasello, 2019). Looking at when subjects choose to monitor a partner's actions could help to tease this apart from social learning.

This study is an encouraging first step, but with so few subjects in each group, and only a subset of those producing the behaviour of interest (flipping the see-saw), a much larger study sample is required with more experimental power to make clear conclusions about chimpanzee incidental action learning during co-ordination, and what this means for how they represent joint tasks. At the moment, we may cautiously infer that during joint tasks with two-actions, chimpanzees learn about their partner’s actions which may help to recreate them when they become solely responsible for both parts of the task. Conversely, when the task is an independent one with the first action completed by an object, chimpanzees may only learn about apparatus affordances and later emulate this by finding other means to manipulate it into its end-state. With only this small sample, however, and only two conditions, it is difficult to infer how these results may generalise beyond these individuals and greater experimental power and further control conditions are required.

Chapter 4: Do chimpanzees consider action effort?[5]

Summary

Previous research shows that, when presented with a cooperative apparatus or a solo apparatus, chimpanzees prefer to work alone. When the reward for working alone is less than that for collaborating, however, chimpanzees choose to work with a partner. This begs the question of what other factors, aside from reward value, contribute to the decision to collaborate or not. This study aimed to develop a paradigm which could test whether chimpanzees may consider action effort or efficiency in these decisions, for example, whether they may be more inclined to collaborate on a task requiring lots of physical effort. As a first step, I assessed whether chimpanzees showed a preference for high or low effort when working alone. Chimpanzees could choose to work on either a high or low effort puzzle box apparatus to access a food reward by moving it along one or three levels. No preference was found for either the low or high effort option. To confirm that chimpanzees understood the selection task, and to investigate whether they were able to plan ahead when choosing which box to approach, I implemented a version in which one box was blocked and thus impossible to access food from. Almost all subjects approached the possible box most often in this task. When presented with the high and low effort options in a repeat of the first experiment after the experience with an impossible box, the lack of preference remained. These findings suggest that chimpanzees are not always motivated to reduce effort, or lack the planning ability to do so within this paradigm.

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[5] This project was a collaboration with Louise Mackie and Sophie Edwards who helped to design and implement a pilot version of this task.

Introduction

Chimpanzees seem to differ from humans in motivation to engage in joint tasks. Despite successfully cooperating in different settings, when given the option to complete a task alone, or with a conspecific partner, chimpanzees choose a solo option. A joint task solution is rejected even when it results in obtaining a food reward faster (Rekers et al., 2011) and only becomes the favoured option when the reward is higher for collaboration (Bullinger et al., 2011). This is in contrast to humans, as even from a young age we are socially motivated to work together; we choose to work as a pair rather than alone (Rekers et al., 2011), and do so even if individual action would be more effective (Curioni et al., 2022). The reasons behind chimpanzee's preference for working alone are currently unknown.

Great apes have shown a tendency to attempt to reduce the physical effort of a task. In the wild, some chimpanzees consider energetic costliness of travel paths when traversing their environments (Green et al., 2019). In an experiment with pairs of chimpanzees in a captive population, when pulling a heavy apparatus, subjects waited longer to begin pulling, preferring instead to let their partner complete the first action which was most effortful (Sánchez-Amaro et al., 2016). Furthermore, gorillas in a captive setting have also shown a sensitivity to effort consideration. In an information seeking paradigm with food hidden inside occluded tubes, gorillas were less likely to seek information in trials which required greater effort to peek (Gazes et al., 2022). Great apes seem to be sensitive to how effortful a task may be, and seem to attempt to minimise the amount of effort they exert.

In joint tasks, humans prioritise co-efficiency over individual effort, indicating co-representation. Co-representation has been described as simultaneously thinking about one's own and one's partner's task and actions, which can aid coordination and is evident in some tasks across several primate species (Miss & Burkart, 2018; Miss et al., 2022). In current paradigms, such as the Joint Simon task, co-representation hinders task performance and so individuals with greater co-operative abilities who may more easily distinguish between their own task and another's task may show lesser co-representation effects. Miss et al. (2022) have suggested implementing paradigms in which co-representation is beneficial to the success of the cooperative task. In a virtual ball passing game, human participants tasked with choosing the route the ball took chose the shortest overall route, rather than attempting to minimise their own or their partner's route (Török et al., 2019) This provides an example of a paradigm in which co-representation leads to co-efficiency considerations which benefit the joint task goal. Humans consider efficiency of the joint task, but what roles do effort and efficiency play in chimpanzee's decisions to engage in joint tasks?

Previously, primates have had success with vertical maze apparatuses. Chimpanzees are able to plan ahead to avoid food falling into traps, at least when no tool is required (Seed et al., 2009). Orangutans and bonobos can, in some cases, plan routes to move food through multiple levels of a puzzle box, at least when they do not have to inhibit touching the food first (Tecwyn et al., 2013). Chimpanzees have also shown success with virtual versions of this task, sometimes performing comparably to human children and outperforming monkeys (although the authors note that the chimpanzees in this sample had extensive testing experience), (Beran et al., 2015). Further, young chimpanzees were able to plan two steps ahead when choosing a route for their food reward to move through levels of a puzzle box (Völter & Call, 2014). Given this body of work, I chose a vertical maze apparatus which did not require the use of a tool, nor the inhibition of touching a food reward, to study effort preferences in chimpanzees.

In order to study whether action effort affects chimpanzees’ decision to work alone or with a partner, and whether chimpanzees consider action efficiency when choosing whether to collaborate or how to distribute a task, it is first important to consider whether the population under study have a preference for minimising their own action effort. To this end, I designed a task in which chimpanzees could choose between two puzzle box apparatuses: one requiring a higher effort to obtain a food reward, and another requiring less effort. After initially finding no preference between the two boxes, I implemented a second experiment in which chimpanzees chose between a possible and an impossible (blocked) apparatus. This was to determine whether or not subjects understood the choice procedure, and whether they were able to check the options before making their selection. The first experiment was then repeated after the exposure to the blocked box experiment to assess whether or not chimpanzees would show a preference between the high and low effort boxes, after having experienced some training to plan before a selection.

Methods

Subjects

Nine chimpanzees participated in this study (3 females and 6 males, mean age 29.0 years [SD = 10.8, range = 7.8 – 45.8] at the beginning of data collection), shown in Table 5. Eight subjects had experience with a pilot version of this task in which they made choices between left and right routes in a single puzzle box.

Table 5: Subject demographic information.

Name	Sex	Age (years)
Velu	M	7.8
Qafzeh	M	30.1
Louis	M	45.8
Lib	M	23.2
Frek	M	28.5
Kilimi	F	29.2
Eva	F	41.3
Edith	F	26.0
Paul	M	29.0

Subjects were housed at the Budongo Research Unit (BRU) in Edinburgh Zoo, Scotland. Housing details for Edinburgh Zoo can be found in Chapter 2.

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 was also approved by the BRU committee (consisting of the Zoo Research Liaison Officer, the Scientific Director, and the Research Coordinator) as well as by the School of Psychology and Neuroscience Research Ethics Committee at the University of St Andrews.

Apparatus

The apparatus consisted of two wooden vertical maze puzzle boxes (60cm wide x 44cm tall, see Figure 12). The food reward (a grape frozen in a $4cm^3$ juice ice cube) could be moved along each level of the puzzle box, and fall onto the level below when it reached the gap in the current level. The size of the mesh through which the subjects manipulated the apparatus and food reward, and the size of the gaps between the levels, allowed enough space to move the food reward along each level with a finger but not enough room to pull it out until it had reached the bottom. Once the food reward was at the bottom of the puzzle box, subjects could retrieve it. One puzzle box had three levels that the subjects had to move the food reward down to be accessed (high effort puzzle box), the other had only one level (low effort puzzle box). For Experiment 2, a cover made of wood and laminate was used to block access to one puzzle box at a time, stuck on with Velcro to be easily removed between blocks of trials (see Figure 13). Testing took place at three testing panels: one puzzle box was presented at the left panel, one at the right panel, and I sat at the central panel (see Figure 14).

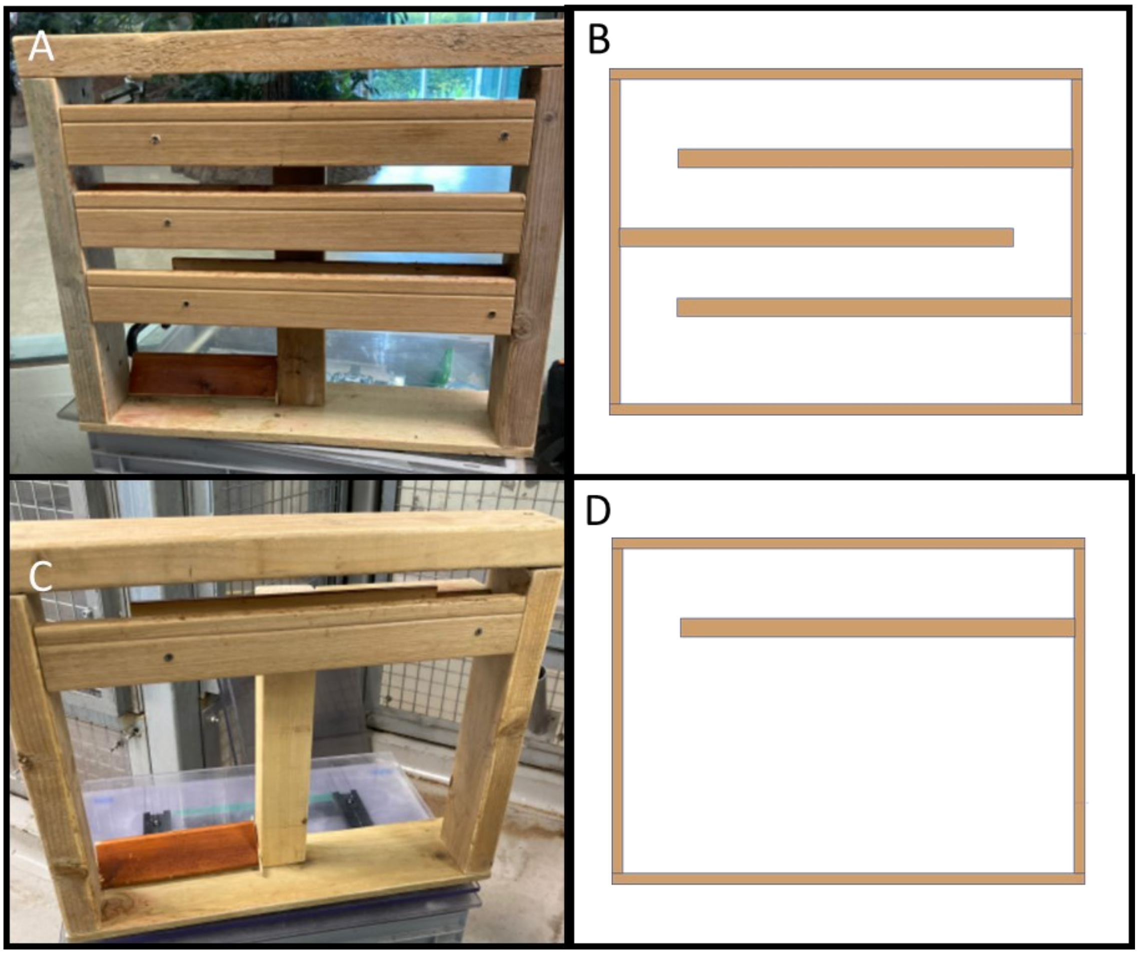

Figure 12: Top left (A): High effort puzzle box with three levels. Top right (B): Schematic of levels in high effort puzzle box. Bottom left (C): Low effort puzzle box with one level. Bottom right (D): Schematic of level in low effort puzzle box.

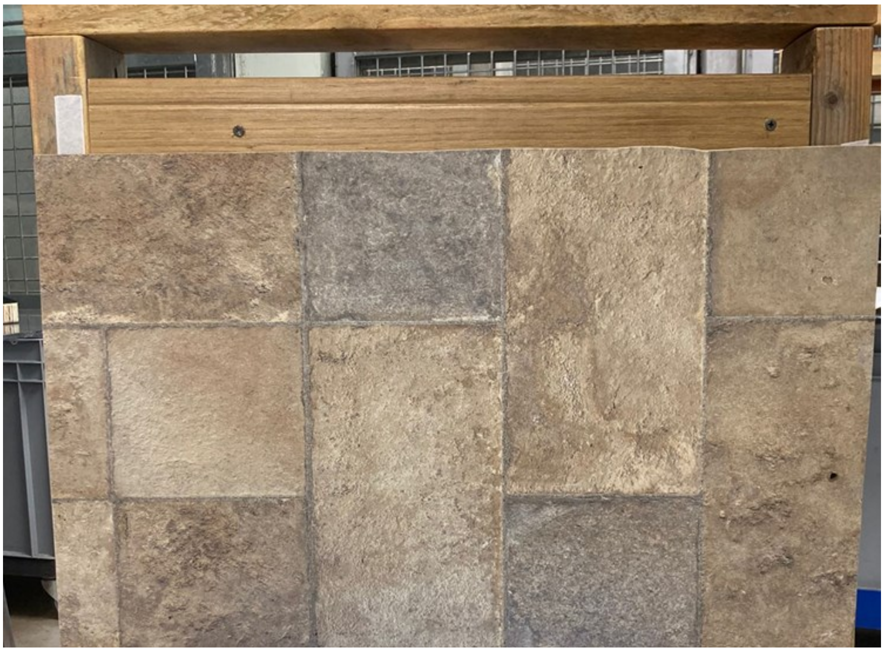

Figure 13: Puzzle box with cover blocking access beyond the first level, used for the 'impossible', blocked puzzle box in Experiment 2.

Figure 14: Experimental set-up from the experimenter's point of view. Yellow X indicates the central panel, which marks the starting position of each subject, and where the experimenter sat. The high effort puzzle box is at the left panel and the low effort box is at the right panel.

Procedure

Puzzle box Training:

Before beginning the experiments, subjects were given experience with both puzzle boxes. I presented subjects with one box at a time (low or high effort) at either the right-most or central testing panel. Subjects received 24 trials in blocks of 6 trials: 6 trials of the high effort box on the left and right, respectively, and 6 trials of the low effort box on the left and right, respectively. I counterbalanced the order of blocks between subjects.

Food follow training:

After the training, subjects received 'food follow training' to confirm that subjects would follow the food rewards from the central panel to the left or right panels. All subjects received four trials and followed the food in all of them, other than one subject (male, Louis) who required two extra trials as he did not initially follow the food. I held one piece of food at the central panel and moved to the left or right panel (randomised between trials), and placed it on a table accessible to the subject. For the first two trials, I only moved the arm required to place the food on the left or right table. For the following two trials, I used one food reward again, but now I outstretched both arms to the left and right, not just the one holding and moving the food, to confirm that subjects were following the food and not only the arm gesture.

General experimental procedure

I presented trials in randomised blocks of 6, such that the low/high effort and/or possible/impossible puzzle boxes swapped sides (left or right) every 6 trials. During the experiments, whereby selections were made between two boxes, subjects always started each trial at the central testing panel. Subjects were moved to the central testing panel either by calling their name, gesturing, showing them food rewards, and/or offering them juice. Once a subject was ready and attentive at the central testing panel, and no other subject was in close proximity to either apparatus, I showed the subject two food rewards, then slowly moved them to above each puzzle box, such that I sat with both arms outstretched to their left and right, holding food rewards above each box. If subjects did not move immediately to one box, I waved my arms up and down slightly and asked: ‘which one?’. If the subject still did not make a selection, I moved the food rewards back to the centre and started again. Once the subject moved to one puzzle box, I took this as their selection; moving their hand or part of their body towards a box was not counted, only movement of the entire body to sit in front of a box counted as a selection. Once a subject had made their selection, I placed the food reward in the top of that box, and pushed the box against the mesh window for the subject to access the box and move the food reward down the levels. Subjects received 24 trials of each experiment.

Experiment 1: low or high effort

I placed the low effort and high effort boxes at the left and right windows, respectively. I counterbalanced the starting side (left or right) of each box between subjects, and the sides where I placed boxes was swapped every 6 trials for each subject. Subjects participated in this experiment twice: once before Experiment 2 (henceforth referred to as Experiment 1A) and once after Experiment 2 (henceforth referred to as Experiment 1B).

Experiment 2:

I attached a cover made of wood and laminate to the front of one puzzle box to block access beyond the first level (see Figure 13). I counterbalanced blocked access between subjects such that half began with the low effort box blocked, and half with the high effort box blocked. I also counterbalanced the blocked side between subjects: half began with the box to their left blocked, and the other half began with the box to their right blocked. Each subject received 6 trials of the following:

- High effort box blocked, on the left
- High effort box blocked, on the right
- Low effort box blocked, on the left
- Low effort box blocked, on the right

I presented these trials in blocks of 6, and counterbalanced the order between subjects.

If the subject chose the box they could access, the procedure was as above. If the subject chose the box that was blocked beyond the first level, once they had moved the food reward down the first level to the blocked part of the box, I waited approximately 3 seconds then pulled the box back, removed the food reward, said ‘oh no’, and removed the food reward before showing the food to the subject. In cases in which the subject did not move the food reward when the blocked box was pushed forwards, I waited approximately 5 seconds, then pulled back the box, removed the food reward, said ‘oh no’, and removed the food reward before showing the food to the subject.

An example video can be found for each experiment via the following link: https://osf.io/k59rd/?view_only=64f475b4458c4af288563f988bebf8e6

Data processing

I live coded subjects’ choices of left and right during testing sessions. A separate coder blind-coded a pseudo-randomly selected subset of 22% of sessions (6/27 sessions; two sessions from different subjects for each of the three experiments) from videos of testing sessions. I evaluated consistency in coding using Cohen's κ for judgements on the side selected, and found excellent agreement: $\kappa = 0.985$, $p < .001$. Analyses, visualisations, and model formation followed the same procedure as laid out in Chapter 2.

Results

Experiment 1A:

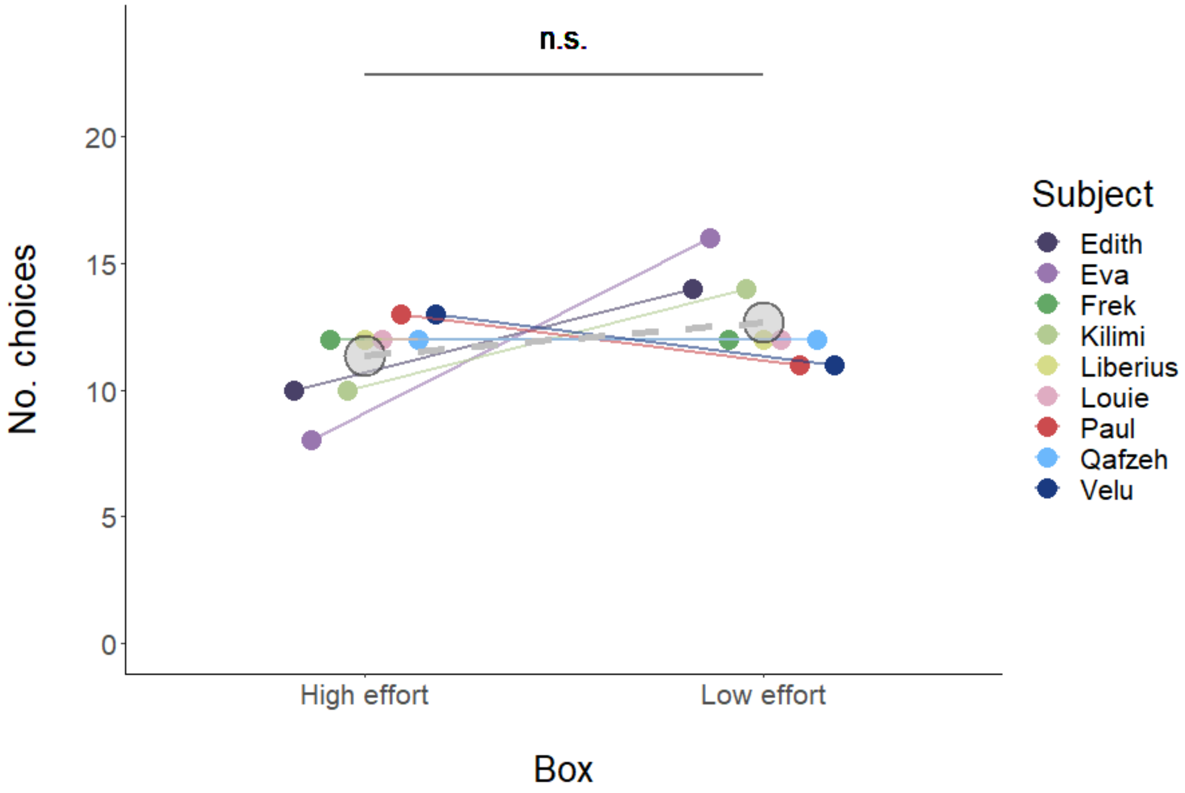

Figure 15: Number of choices of either the high or low effort puzzle box across 24 trials of Experiment 1. Coloured dots and lines show individual data for each subject, grey dots and dashed line show the group mean.

Experiment 1A: A binomial GLMM [Side chosen ~ Box position + (1|Subject)] showed no effect of where the high effort box was placed (left or right) on subjects' choices (left or right): χ2 (1) = 1.32, *p* = .25, OR = 1.41, (Figure 15). Subjects showed no preference for either the high or low effort box.

A second, exploratory analysis looked at whether subjects' behaviour could be explained by side biases. That is, currently the data show no preferences from subjects, but it is not clear whether they were choosing randomly or whether they were choosing the same side each time. As the sides of the boxes were counterbalanced and present on the left and right 12 times each (in blocks of 6), if a subject has a strong tendency to choose the same side across trials, this would present as no preference when only looking at choices of high and low effort. I used binomial GLMs to assess subjects' individual side preferences (Box choice (high/low) ~ Box position (left/right)). Results are shown in Table 6. All subjects except Paul, Velu, Edith, and Eva demonstrated clear side preferences. For the remaining 5 subjects, all but one (Qafzeh) demonstrated a bias for the box to their right/to the experimenter's left.

Table 6: Outputs of individual GLMs for side preferences in Experiment 1A.

Subject	**Effect of box side on choosing box**	
Liberius	χ2 (1) = 33.27	*p* < .001
Louis	χ2 (1) = 33.27	*p* < .001
Frek	χ2 (1) = 19.50	*p* < .001
Paul	χ2 (1) = 0.17	*p* = .68
Velu	χ2 (1) = 1.53	*p* = .22
Qafzeh	χ2 (1) = 33.27	*p* < .001
Kilimi	χ2 (1) = 21.79	*p* < .001
Edith	χ2 (1) = 0	*p* = 1
Eva	χ2 (1) = 3.10	*p* = .08

Experiment 2:

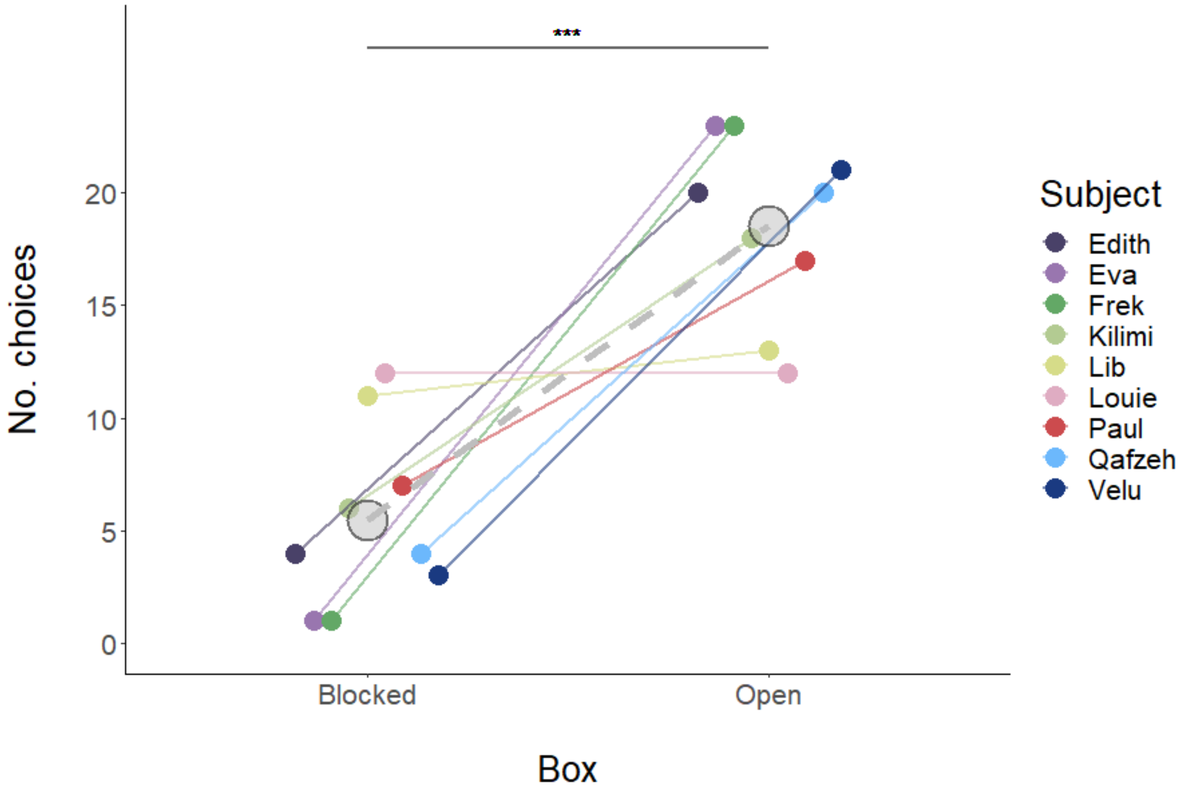

Figure 16: Number of choices of either the blocked or open puzzle box across 24 trials of Experiment 2. Coloured dots and lines show individual data for each subject, grey dots and dashed line show the group mean.

Experiment 2: A binomial GLMM [Side choice ~ Blocked side (left/right) + Blocked box (high/low effort) + (1|Subject)] showed a significant effect of which side was blocked (left or right) on subjects' choices (left or right): χ2 (1) = 101.80, *p* < .001, OR = 17.90 (Figure 16). The analysis showed no effect of whether the blocked box was low or high effort: χ2 (1) = 0.442, *p* = .51. Subjects chose the box they could access over the one they could not, and this was not affected by which box was blocked.

To assess which individuals preferentially chose the open box in Experiment 2, I used binomial GLMs to assess individual preferences [Side chosen ~ Blocked side (left/right) +

Blocked box (high/low effort)]. All subjects except Louis and Liberius showed an effect of where the blocked box was on their side selections (Table 7).

Table 7: Outputs of individual GLMs for Experiment 2

Subject	**Effect of blocked box location on side selection**	
Liberius	χ2 (1) = 1.48	*p* = .22
Louis	χ2 (1) = 0	*p* = 1
Frek	χ2 (1) = 27.53	*p* < .001
Paul	χ2 (1) = 4.68	*p* = .03
Velu	χ2 (1) = 15.63	*p* < .001
Qafzeh	χ2 (1) = 16.07	*p* < .001
Kilimi	χ2 (1) = 10.81	*p* = .001
Edith	χ2 (1) = 16.07	*p* < .001
Eva	χ2 (1) = 27.53	*p* < .001

Experiment 1B:

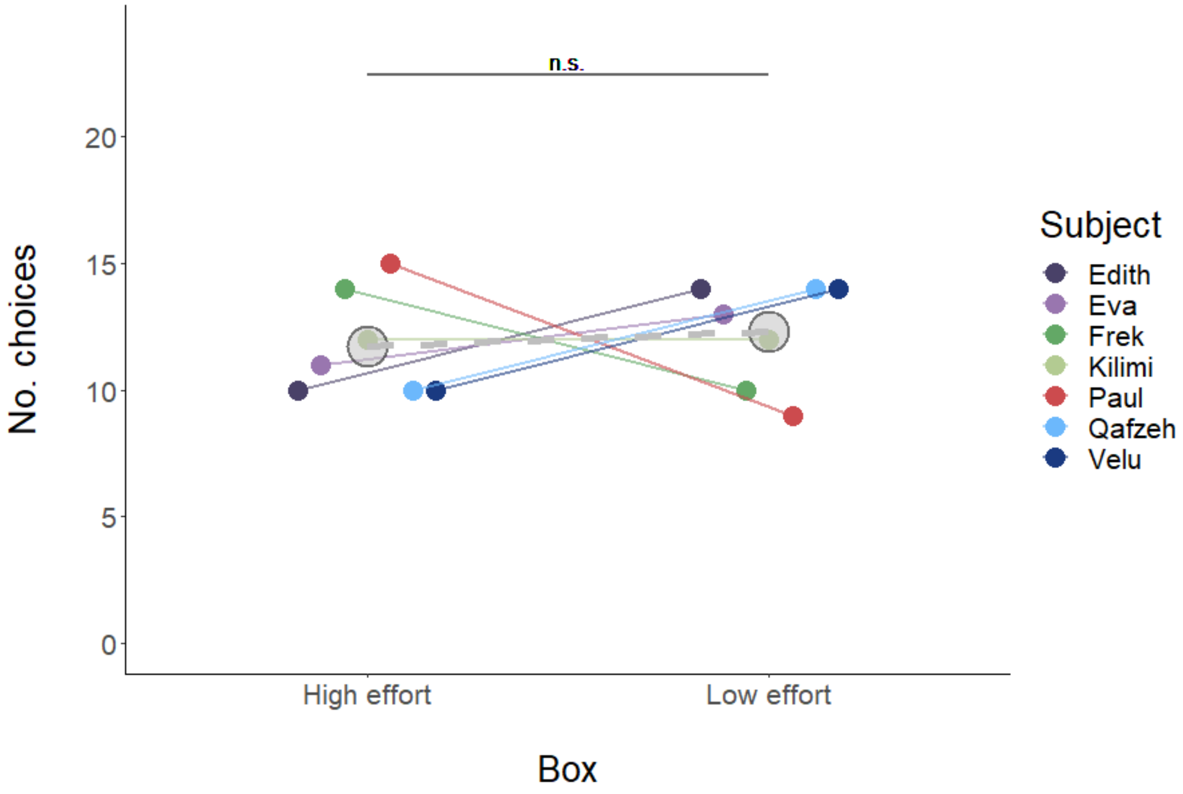

Figure 17: Number of choices of either the high or low effort puzzle box across 24 trials of Experiment 1B in subjects showing a preference in Experiment 2 (Louis and Liberius removed). Coloured dots and lines show individual data for each subject, grey dots and dashed line show the group mean.

As two subjects (Louis and Liberius) did not show a preference in Experiment 2 for the blocked or open box (shown in Figures 15-16 in pink and lightest green), and instead demonstrated pervasive side biases, I removed them from the analysis for Experiment 1B. A binomial GLMM including only subjects who showed a preference for the open box in Experiment 2 [Side chosen ~ Box position + (1|Subject)] showed no effect of where the high box was placed on subjects' choices: χ2 (1) = 0.20 *p* = .65, OR = 1.08, (Figure 17).

As previously, a second, exploratory analysis looked at whether subjects' behaviour could be explained by side biases. I used binomial GLMs to assess subjects' individual side preferences [Box chosen (high or low effort) ~ Box position (left/right)]. Results are shown in Table 8. All subjects except Qafzeh demonstrated significant side preferences. For the remaining 6 subjects, 4 showed a preference for the box to their left (Paul, Velu, Edith, and Eva) and 2 showed a preference for the box to their right (Frek, and Kilimi).

Table 8: Outputs of individual GLMs for side preferences in Experiment 1B.

Subject	**Effect of high effort box on the left on choosing high effort box**	
Frek	$\chi2\ (1) = 12.22$	$p < .001$
Paul	$\beta = 1.58$, $\chi2\ (1) = 4.64$	$p = .03$
Velu	$\chi2\ (1) = 21.79$	$p < .001$
Qafzeh	$\chi2\ (1) = 0$	$p = 1$
Kilimi	$\chi2\ (1) = 33.27$	$p < .001$
Edith	$\chi2\ (1) = 21.79$	$p < .001$
Eva	$\chi2\ (1) = 26.22$	$p < .001$

Discussion

Chimpanzees in this study were given the option to engage in either a high or low effort task. Once a selection was made, subjects could move a food reward down either one or three levels of a puzzle box apparatus which acted as a vertical maze. Subjects showed no preference for either of the boxes and instead often perseverated on the same side across trials. A second experiment looked at whether this perseveration would persist when one box became impossible to retrieve food from, by blocking access to lower levels. Most subjects overcame their side biases and showed a preference for the available box. For two subjects, however, the side biases persisted, and they showed no preference for the blocked or open box. Experiment 1 was then repeated after subjects had gained experience from the blocked boxes to investigate whether they showed any preferences now that they had gained experience with checking the boxes before choosing a side. No preference was found, and most subjects returned to having side biases once both boxes became possible to use. This is a strategy that is suggested to reflect contentedness with less rewards in primate cognition studies which here may indicate a contentedness with putting in slightly more effort on half of the trials (Whitham & Washburn, 2020). These findings indicate that captive populations of chimpanzees do not always try to find the easiest or least effortful solution to a problem.

It is possible that in this study the task was simply enjoyable, or intrinsically motivating, to chimpanzees. Subjects may have found it rewarding to move the food down the levels of the box, and were thus not motivated to select an option which reduced this. Indeed, previous research has demonstrated that animals do not always choose the easiest option for accessing a food reward; 'contrafreeloading' behaviour has been found across species, including African grey parrots (Smith et al., 2021), kea (Smith et al., 2022), pigeons (Neuringer, 1969), rats (Carder & Berkowitz, 1970; Jensen, 1963), and even chimpanzees (Menzel, 1991). While choosing to work more for a food reward may seem to be a sub-optimal strategy, other considerations such as a desire to play or seek information may also count in these choices. Taking a purely economic view that a higher or easily accessed reward is always the rational choice may lead to classifying choices as errors without a full picture of why the choice was made (Menzel, 1991).

It is challenging to find a task which strikes the balance between being motivating enough for chimpanzees to voluntarily engage with, but difficult enough to motivate them to seek to minimise effort. The apparatus in this study mimics a foraging enrichment apparatus found in primate enclosures across zoos, and so is deemed cognitively enriching (Padrell et al., 2022; Clark et al., 2019). It is possible that with a different experimental set-up, such as pulling heavy or light ropes, or reaching higher or lower, chimpanzees may demonstrate effort minimising behaviour. Another possible reason for chimpanzees' lack of effort minimising in this study is that the desire to be efficient may not always be present in captive populations. In captivity, chimpanzees have consistent access to food and, each day that the experiment was conducted, the apparatuses were present for approximately 3.5 hours. It is possible that, in these circumstances, chimpanzees felt no need to prioritise conserving energy and did not have a sense of time pressure. Future work could contrast this task with a delay of gratification task in which chimpanzees have to wait longer for a reward from one apparatus than another, and assess preferences here. It may be that as long as they have a task to occupy themselves with (here, working on the levels of the boxes), chimpanzees do not mind a larger time gap between selection and reward; this may not be the case if their only task is to wait (although some research suggests that chimpanzees can be quite patient, such as Rosati et al., 2007).

Planning abilities may also have affected the results here. It may be that, with the cover blocking one apparatus, it was easy to notice this obstruction and incorporate it into a decision. In contrast, with the different numbers of levels, the visual difference between the apparatus options was more subtle. Avoiding a salient barrier may involve a faster learning process than learning to avoid three levels compared to one level of the puzzle box. It may be that the chimpanzees in this sample do prefer to minimise effort, but were not able to plan accordingly with this set-up. With a clearer difference between the apparatus options, preferences may be revealed.

Many chimpanzees in this study perseverated on one side across trials, showing little behavioural flexibility in responses. Primates have been shown to stick to one strategy if they find that it works (Pope et al., 2020). This is consistent with the pattern of results here; as long as rewards could be accessed from both boxes, most subjects stuck to the same side throughout trials. Once one box became impossible to retrieve a reward from, most subjects switched to a more flexible strategy. After this experience, most subjects returned to side biases once that strategy produced consistent rewards. This suggests that it was not an inability to switch sides, or a lack of understanding that two options were available. It may have been rather that as long as food was available, despite having to work a little harder on half of trials, most chimpanzees became stuck in their ways and no longer switched between boxes (although note that there were individual differences here).

It is important to consider the selection bias of the sample in this study. All participation from chimpanzees was entirely voluntary. While this is extremely important for ethical data collection with primates, in an investigation of motivation this inherently biases the sample. The subjects engaging with the task were the individuals in the population who were motivated to do so; they may be more motivated individuals. Likewise, the time at which they participated in the task was a time when they chose to do so; they may be particularly motivated to interact with the apparatus in that moment. It may be that the snapshot this study provides into chimpanzee effort considerations is skewed, and other chimpanzees who did not engage with the research, or indeed the same individuals at a different point in time, may behave differently and may be more inclined to reduce the amount of effort they exert. The same sampling bias issue could be applied to many studies with chimpanzees and so these results may nonetheless generalise to the population of chimpanzees engaging in cognitive tasks in captivity. However, caution should be taken when generalising these findings, and both inter- and intra- individual variations may influence behaviour in ways not captured here.

In summary, chimpanzees showed no preference between high and low effort puzzle box apparatuses. This could indicate that chimpanzees are not always motivated to minimise their effort, or that they do not always consider action effort during planning. Future research should consider that chimpanzees in these settings may not always be motivated to find the easiest option. It should not be assumed that great apes in captivity will always try to access a food reward as quickly and as easily as possible; at times they may enjoy engaging with the apparatus, or be indifferent to how long or how much effort it takes to get a reward. This could have implications for designing enrichment items provided to captive primates, as well as for experimental designs.

Chapter 5: Spatial frames of reference and landmark use during virtual environment navigation in chimpanzees[6]

Summary

Virtual environments offer the opportunity to study large scale spatial cognition in captive ape populations. One of the steps in validating this method is studying how apes represent these environments. In previous, small-scale spatial cognition tasks, apes have demonstrated a tendency to use allocentric frames of reference. That is, great apes encode objects in relation to other aspects of the environment rather than in relation to themselves. This study looked at landmark use and frames of reference during virtual environment navigation in chimpanzees. Across three experiments, zoo-housed chimpanzee subjects interacted with a virtual environment via a touchscreen interface to move an avatar around an arena in search of virtual food, for which they were rewarded with real food. A goal location and a distractor location stood equidistant from the avatar at the start of each trial, and through a series of training stages subjects learnt to always navigate to the same location to find the food. In experimental conditions, subjects were also given experience moving their avatar around the entire arena and viewing it from multiple angles, whereas in control conditions this experience was not provided. In each condition of the three experiments, different landmarks were present. In Experiment 1, the experimental condition included a tree in the target location as a proximal coincident landmark, and the control condition contained no landmarks. Experiment 2 used a central statue of either a bird or squirrel in both conditions, as a proximal non-coincident landmark. Finally, in

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[6] This project was a collaboration with Matthias Allritz, Ken Schweller, Daniel Haun, and Emile Rapport Munro. Some of the data was collected by Matthias Allritz, Emilie Rapport Munro, and research interns. The supplementary video was put together by Matthias Allritz.

Experiment 3, distal landmarks stood in the North and South of the arena which were either familiar (experimental condition) or novel (control condition). Once trained to a criterion to always approach the same goal location, subjects were translocated 180 degrees and now faced the locations with the opposite view to that in the training stages. When a proximal landmark was present at the goal location, apes were able to use this to find food from the opposite angle. However, prior experience with virtual landmarks played a key role here. In the following two experiments, apes were unable to use spatial relations to landmarks to find food. Results suggest that experience approaching a landmark from multiple views may be needed to use allocentric encoding in virtual spaces.

Introduction

The way in which aspects of an environment are mentally represented can differ by the referent points used. A distinction can be made between ‘frames of reference’ used in spatial cognition; we can use information about how a target location relates to oneself (“egocentric”) and/or how it relates to other aspects of the environment (“allocentric”) (also referred to as “body-centred” and “world-centred”, respectively), (Fernandez-Baizan et al., 2019b; Bullens et al., 2010). It is thought that, in humans, the allocentric framework is not fully developed until around 7 years of age. First, we learn to recognise landmarks, but with no directional information. Secondly, we learn to follow a route with consecutive landmarks (for example, learning that when I see the school, I turn left). Finally, we develop full allocentric orientation and can organise and memorise landmarks in a mental map (Fernandez-Baizan et al., 2019b), although some research notes that on certain tasks children do not reach adult-like performance and orient themselves fully until aged 10 (Bullens et al., 2010). Nevertheless, some allocentric orientation can be seen from a young age in humans. Fernandez-Baizan et al. (2019) reviewed 49 studies and found that, although an egocentric framework seems to develop first, infants from 4.5 months can use simple landmarks, and from 5 years onwards can integrate spatial information from different cues. Early infant research using a simple set-up in which infants turned their heads in expectation of an event to their left and right, and were then moved to look from the reverse side, has also suggested that humans firstly encode locations egocentrically (at 6 to 11 months), and shift to allocentric encoding (here termed 'objective') at 16 months (Acredolo, 1978). Taken together, it seems that in humans, egocentric strategies emerge first but from a relatively young age, some allocentric strategies can also be employed and continue to develop throughout childhood.

Cultural context also shapes spatial frames of reference, and may influence the way we encode locations. The language preferentially used to describe spatial relations varies between cultures (Levinson, 2003), and it has been suggested that language and culture impact our spatial-cognitive strategies (Haun et al., 2006). For example, in a cross-cultural comparison of Dutch and Hai||om adults and children, participants preferentially used spatial search strategies consistent with the preferential descriptions in their native languages. When searching among an array of cups first from one side, then from a position reversed 180°, Dutch participants preferred an egocentric strategy (i.e., choosing the cup to their left) whereas Hai||om participants preferentially used a geocentric (a form of allocentric) strategy (i.e., choosing the cup in the North-West), (Haun et al., 2006).

Across great apes presented with an analogous task with three adjacent cups to find a reward inside, all four species showed a preference for an allocentric strategy over an egocentric strategy (Haun et al., 2006). This is consistent with other work showing that chimpanzees can locate hidden food when they themselves approach it from a new angle (Hoffman & Beran, 2006). Additionally, work with chimpanzees, bonobos, and orangutans showed a possible allocentric strategy employed by these apes when searching in different arrays of cups for a reward (Hribar et al., 2011), although another study found that performance decreased when the number of food items to find increased to two (Beran et al., 2005a). Allocentric strategies have also been shown across all four great ape species in tasks in which an array of cups rotated, translocation tasks in which subjects approached from the opposite side to baiting, and trials with both these manipulations (Albiach-Serrano et al., 2010). Chimpanzees outperformed other species in this task, showing the highest accuracy at tracking a hidden food reward. However, chimpanzee performance on rotational displacement tasks is poorer when the rotations are not seen (Okamoto-Barth & Call, 2008). In strepsirrhine primates that vary in level of frugivory, the most frugivorous primates (which chimpanzees are also considered, Wrangham, 1986; Tweheyo & Lye, 2003) show more use of allocentric spatial strategies than more folivorous species, suggesting that feeding ecology may also shape spatial cognition (Rosati et al., 2014). It appears that, while in humans our frames of reference are somewhat dependent on our language and culture, in our closest living relative species, allocentric strategies are preferred.

Landmarks within an environment can be used as allocentric cues to locate a target, and this strategy can be seen across several animal species (ants: Collett, 2010; sting rays: Schluessel & Bleckmann, 2005; sticklebacks: Odling-Smee & Braithwaite, 2003; goldfish: Warburton, 1990; pigeons: Cheng, 1989; hummingbirds: Pritchard et al., 2016; capuchins: Garber & Paciulli, 1997, to name but a handful). Landmarks can be defined based on their proximity to a target in the following ways: coincident (located at the target position), proximal non-coincident (located near but not at a target position), and distal non-coincident (located further from a target location), (Fernandez-Baizan et al., 2019b). Consider locating your car in a large carpark. You could use a parking space number above the car as a coincident cue, a ticket machine to the left of your car as a proximal non-coincident landmark, or perhaps a fire escape sign further away that you remember the approximate angle and distance of from the car as a distal non-coincident cue. Infants from as young as 4.5 months are able to use coincident landmarks if they've seen an environment from multiple viewpoints, from 8.5 months can use non-coincident landmarks, and from 2-3 years can use distal non-coincident landmarks (Fernandez-Baizan et al., 2019b). In a previous touchscreen task, orang-utans were able to use landmarks in a two-dimensional environment (Marsh et al., 2011). Capuchins have also demonstrated an ability to use coincident landmarks when a simple associative rule can be applied, but not when a more complex rule is required when a landmark is placed nearer a distractor location (Potì, 2000). Potì noted that capuchins initially seemed to adopt an egocentric strategy (referred to as a 'self-referenced frame'), and an allocentric strategy (referred to as an 'external frame') required to solve the task had to be learned. Furthermore, cotton-top tamarins are able to use the spatial relations between multiple landmarks to find food (Dolins, 2009) and wild capuchins can learn to use a landmark placed by experimenters, and are able to quickly learn spatial locations of feeding sites (Garber & Paciulli, 1997). In sum, landmarks are a key part of spatial cognition in many species, and different types of landmarks may influence which frame of reference is applied.

Studies of human spatial cognition have previously employed virtual environments for studying spatial frames of reference and landmark use. León et al. (2014) presented a desktop virtual environment to children and found that they were able to use allocentric strategies to identify correct boxes in a room with distal landmark features on the walls from different starting points, and that performance improved after 5 years of age. Additionally, Negen et al. (2018) used a design in which children were translocated to a new point in a virtual environment after learning the location of a target, which the authors call a ‘strict test for allocentric coding’. In this virtual allocentric translocation task, only older participants aged 4-4.5 years were successful. These studies reported similar developmental trajectories to the findings of the review by Fernandez-Baizan et al. (2019), suggesting that allocentric strategy use in virtual contexts reflects findings across other studies. Furthermore, research has shown that human adult participants demonstrate similar route-finding, direction judgement, and relative distance judgements in a desktop virtual environment to the equivalent real-life environment (Ruddle et al., 1997). Moreover, virtual navigation on tablets and smartphones has been shown to correlate with real-world wayfinding abilities in multiple locations (Coutrot et al., 2019). Given the previous successes of using virtual environments in developmental studies, and given that they can be delivered non-verbally, virtual environment tasks could also prove useful in comparative work.

Landmarks appear to play an important role in route-learning in virtual environments for both children and adults. Children are better at retracing routes when they can use virtual landmarks compared to when only directional information is available (Lingwood et al., 2015). Human adults in one study were only able to take shortcuts in virtual environments when landmarks were present, and could not take shortcuts when landmarks were absent (Foo et al., 2005). As landmarks appear to be important cues for virtual environment navigation in humans, studying virtual landmarks may be a sensible starting point for investigating virtual environment navigation in primates.

Field studies of chimpanzee navigation have suggested they can remember multiple food locations, show goal directed travel to food sources, and demonstrate efficient travel routes (Janmaat et al., 2013; Normand, et al., 2009; Ban et al., 2016). However, large-scale navigation in primates is challenging to study in captivity due to the limitations on available space (Normand, et al., 2009). While field studies provide rich data through tracking wild primates, it can often be difficult to see exactly what a focal subject can see, and which cues they may be responding to when making movement decisions (Noser & Byrne, 2014). Experiments in captive settings can often build upon fieldwork and provide more rigorous experimental control, but thus far in navigation research this has not been feasible. Virtual environments may provide a solution to this challenge and allow for controlled, repeated testing on large scale spatial cognition in captive settings. Previous research has shown success with the use of virtual environments with chimpanzees; six subjects learned to approach a coincident landmark to find food from different starting points and angles within a virtual environment and some showed flexibility and were able to switch to a new location once the familiar goal location was empty (Allritz et al., 2022). In another task within a virtual maze, chimpanzees were also able to use visual cues to turn left or right (Dolins et al., 2014). Virtual environments seem to be a viable method for study in primate cognition, and chimpanzees are able to use virtual landmarks as beacons at least when no other distractor location is present.

The aims of this study are twofold. Firstly, this study aims to assess which spatial frames of reference are used during navigation in chimpanzees and whether different virtual landmarks affect these strategies. Secondly, by assessing this I also hope to learn whether chimpanzees are conceiving of this virtual environment as a three-dimensional space which could further validate the use of virtual environments in primate navigation research. I present a virtual translocation task to a relatively large sample of chimpanzees to probe their strategies in finding food in virtual environments. Chimpanzees were presented with two hedges in a virtual arena, one containing food to be collected and the other containing a hole that they fall down, leading to a brief timeout. After an initial stage to learn this reward contingency, a 'transfer test' was implemented in which chimpanzees were translocated to the opposite side of the virtual testing arena and now had to find the correct hedge from the opposite approach. If subjects learned an egocentric strategy during training, this would be demonstrated by continuing to approach the hedge to their left/right. If, however, subjects had learned an allocentric strategy, I would expect them to correctly infer that they were approaching from a new location and enter the correct hedge from this new location. In Experiment 1, a coincident tree landmark was inside the correct hedge in the experimental condition, and no landmarks were present in the control condition. In Experiment 2, a central statue landmark stood between the two hedges, which was either a puffin or a squirrel, and here the experience of viewing the landmarks from multiple viewpoints or only one viewpoint was varied between experimental and control conditions. Finally, in Experiment 3, distal landmarks were placed in the North and South of the virtual arena, and the control condition employed entirely novel landmarks in the transfer test.

This study also acts as an assessment of cognitive flexibility through reversal learning. Reversal learning tests how well a subject can change their response once contingencies change after learning. For example, Piaget's A-not-B task in which an object is hidden under the same cup (of a pair of cups) consistently, and then is hidden in the other cup. Infants struggle to change their response from the initial learning stage until approximately 12 months and instead perseverate on the original reward location (Piaget, 1954). Barth and

Call (2006) showed that all four species of great ape were able to pass this task and show flexible responding with visible and invisible object displacements, and were also able to pass this task when the array of three cups was rotated 180° between baiting and selection. Although, the success rate was considerably lower here than in previous versions of this task with two cups (Call, 2003). In this set-up, apes were only able to learn the contingency when the initial baiting was seen and not when the food location was signalled by a marker on the correct container. Beran et al. (2005b), however, found that three chimpanzees were able to use a marker to infer a food location in a rotation task over a larger number of trials. As previous research suggests that great apes are capable of reversal learning, I will implement appropriate control conditions to account for this strategy.

In Experiment 1, during the transfer test, which serves as a translocation/rotation test, instead of comparing performance to chance, I instead compare performance to a control condition in which no landmarks are present. Here, I can compare the rate of accuracy with a coincident landmark present to how well chimpanzees do when only able to use a reversal learning strategy (with no landmarks present). Experiment 2 uses a central proximate landmark, and the only difference between the experimental and control conditions is the experience of seeing the environment and landmark from several viewpoints in the experimental condition, and only one viewpoint in the control condition. Here, in the control condition it may still be possible to solve the task with an allocentric strategy if subjects can infer that they are behind the central landmark in the control condition. I intentionally chose stimuli which subjects could conceivably imagine from the front and back (faces) and ensured that social stimuli were used in both conditions to account for the attentional power of facial stimuli (Leopold & Rhodes, 2010; Ro et al., 2007). In Experiment 3, conditional discrimination could aid reversal learning, as by this point in the study subjects may have learnt a rule that as soon as a cue in the environment changes, they should change their response. For this reason, I compare performance in the experimental condition with a condition in which completely novel landmarks are used in the transfer test which provide no information about spatial relations to the goal.

Methods

Subjects

A total of 14 chimpanzees participated in this study, although not all chimpanzees participated in each experiment. See Table 9 for details of subjects who did not complete all experiments.

Experiment 1: 14 chimpanzees participated in this study (6 females and 8 males, mean age 30.5 years [SD = 14.2, range = 6.8 – 47.8 years] at the beginning of data collection).

Experiment 2: 11 chimpanzees participated in this study (5 females and 6 males, mean age 31.4 years [SD = 15.9, range = 6.8 – 47.8 years]).

Experiment 3: 8 chimpanzees participated in this study (3 females and 5 males, mean age 32.2 years [SD = 15.8, range = 6.8 – 47.8 years]).

Seven chimpanzees were housed at the Budongo Research Unit (BRU) in Edinburgh Zoo, Scotland, and seven were housed at the Wolfgang Köhler Primate Research Centre (WKPRC) in Leipzig Zoo, Germany. Housing details for Edinburgh Zoo and Leipzig Zoo can be found in Chapter 2.

Four chimpanzees previously participated in a virtual environment experiment involving the use of a virtual tree landmark (Allritz et al., 2022). All subjects had some prior virtual environment experience to train them to move an avatar and collect virtual food.

Table 9: Subject demographics and list of experiments participated in.

Name	Group	Sex	Age (years)	Inclusion	Reason for Incompletion	Participated in Allritz et al (2022)
Frek	EDI	M	27.4	1,2,3	NA	N
Velu	EDI	M	6.8	1*,2,3	NA	N
Louie	EDI	M	44.7	1,2*,3	NA	N
Fraukje	LPZ	F	45.4	1,2,3	NA	Y
Frederike	LPZ	F	47.8***	1,2,3*	NA	Y
Tai	LPZ	F	19.2	1,2,3	NA	N
Alex	LPZ	M	20.2	1,2,3	NA	Y
Robert	LPZ	M	46.2	1,2,3	NA	N
Eva	EDI	F	40.3	1,2	Time constraints	N
Dorien	LPZ	F	40.9	1,2	Passed away	Y
Azibo	LPZ	M	6.8	1*,2	Time constraints	N
Qafzeh	EDI	M	29.4	1	Time constraints	N
Kilimi	EDI	F	28.5	1	Time constraints	N
Liberius	EDI	M	22.9	1**	Time constraints	N

**Did not pass training and not included in transfer test analyses.*
***Did not complete training and only included in location learning analysis.*
****Exact birth date unknown, approximated from birth year*

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 BRU committee, consisting of the Zoo Research Liaison Officer, the Scientific Director, and the Research Coordinator. Research in Leipzig was approved by the WKPRC committee composed of the director of WKPRC, the research coordinator, the head keeper of great ape husbandry, and the zoo veterinarian. The research was also approved by the School of Psychology and Neuroscience Research Ethics Committee at the University of St Andrews.

Apparatus

The touchscreen setup consisted of a solid metal frame with an infrared touch frame and a transparent acrylic panel (19’’ Keytec OPTIR Touch PPMT-IR-019EL in Leipzig, 23’’ Keytec and ProDisplay touch frames in Edinburgh). I mounted a computer monitor (Leipzig: 19’’, AR =

5:4, 1024 x 768, ViewSonic VG930m; Edinburgh: 23’’, AR = 16:9, 1440 × 900, HP E23 G4 FHD and HP E232) behind this to display the virtual environment game to the subjects, and connected this to a duplicated monitor for me to view. The location touched on the screen corresponded to the locations on the monitor mounted behind it by connecting the touchscreen to the experimenter’s computer, and calibrating it using iNexio Touch Drive software. A schematic of the set-up is shown in Figure 20. I placed two speakers just outside of the ape testing area, in the experimenter area, to provide auditory feedback throughout the task. In Edinburgh, I connected a second, smaller monitor to a camera that filmed subjects while using the touchscreen, allowing me to quickly identify subjects whenever they approached the screen.

Virtual environment programme overview:

The virtual foraging game (APExplorer_3D) was programmed in C# with the Unity3D game engine (Schweller et al., 2022). Figures 18-19 show examples of the set up in the virtual environment from the subjects’ viewpoint and Figure 18 shows a chimpanzee interacting with the program. The apes move an avatar around the environment and ‘collect’ virtual fruit, for which they are rewarded with a piece of the equivalent real fruit. The environment is viewed in a first-person perspective and consists of 3D objects presented in 2D, as in many video games. When a location on the screen is touched, the avatar walks in this direction. To allow for orienting on the spot without changing location, when the bottom two corners of the screen are touched the avatar rotates on the spot (see Figure 19 for details). As the avatar moves around the arena, footstep noises are sounded. When a virtual fruit is collected, a reward sound (“tadaa”) is played, and a piece of food is delivered to the ape. When the avatar walks into an obstacle, or into one of the four walls surrounding the arena, it bounces back slightly. Thus, subjects receive constant feedback as every touch elicits some movement and sound, even when the subject is not immediately rewarded.

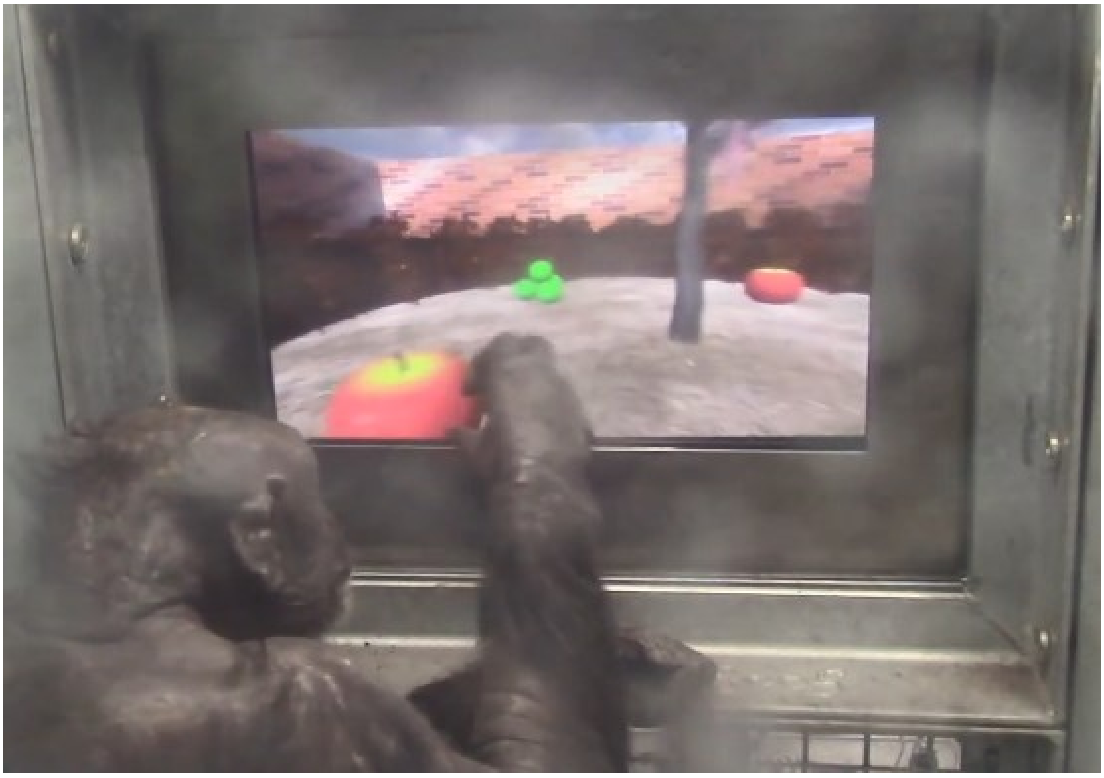

Figure 18: A chimpanzee (Eva) interacting with the virtual environment presented on a touchscreen. Here the subject is approaching virtual fruit and is about to 'collect' a virtual apple.

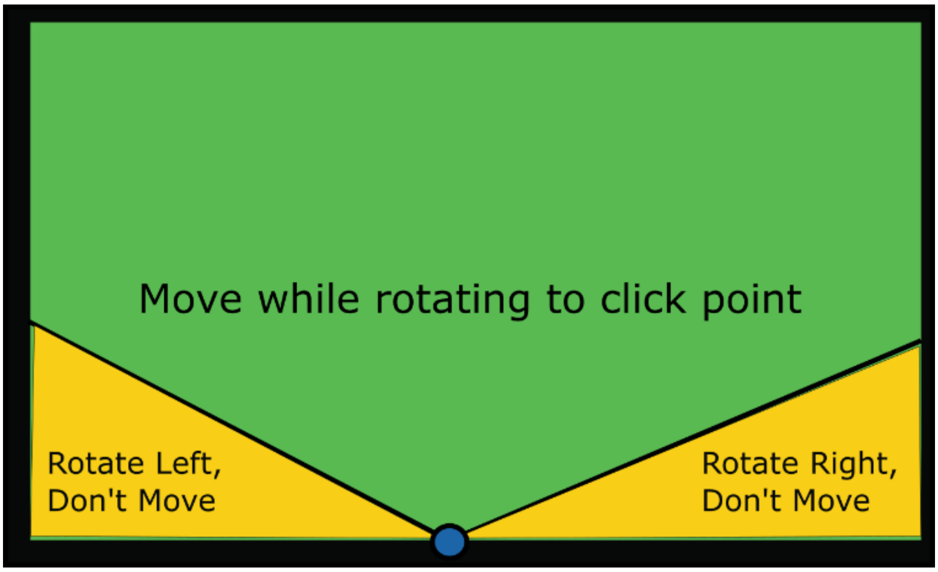

Figure 19: Depiction of the way in which the screen is divided into areas which when touched result in the avatar moving to the location, and areas which when touched result in the avatar turning on the spot (adapted from Allritz et al, 2022.).

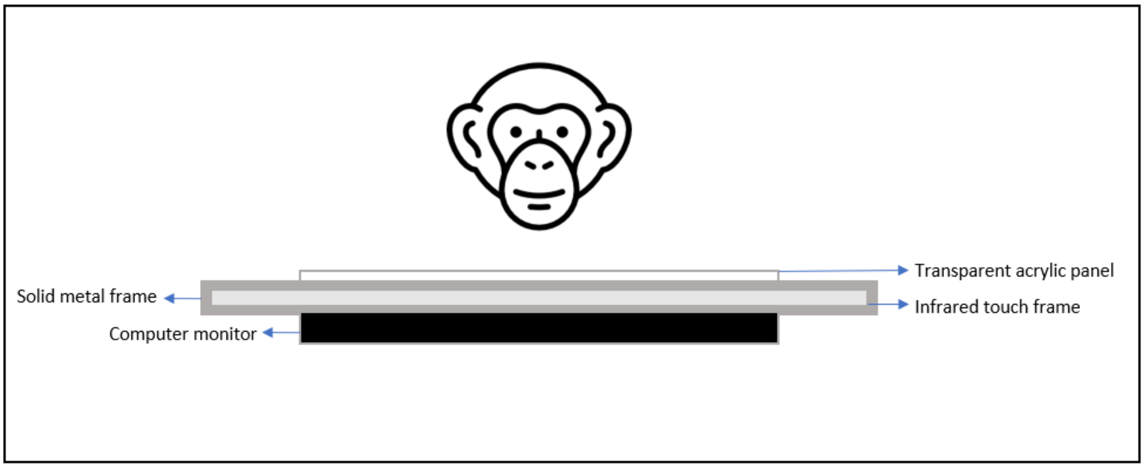

Figure 20: A schematic of the touchscreen testing set-up.

Procedure

Experiment overview: All subjects completed both the experimental and control conditions. I counterbalanced the order of these conditions within each experiment, but the order of experiments remained consistent for all subjects. I kept the order of control and experimental condition constant for each subject for each experiment. That is, if a subject completed the control condition before the experimental condition in Experiment 1, they also completed the control condition before the experimental condition in Experiments 2 and 3. I also counterbalanced the arena assigned to control and experimental conditions between subjects, and kept this consistent for each subject. I counterbalanced the hedge containing the food (West or East) between subjects and kept this constant for each experiment. Details of counterbalancing can be found in Appendix B, Table B1. Details of any deviations from the experimental protocol can also be found in Appendix B, Table B5.

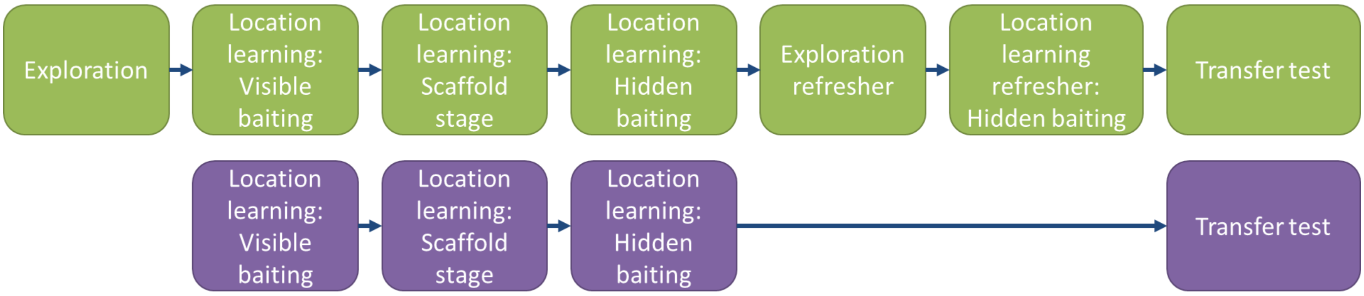

Figure 21: Overview of the study procedure. Green shapes along the top indicate the stages in the experimental condition, purple shapes along the bottom indicate the stages in the control condition.

Experimental procedure for each experiment: Figure 21 presents the order of stages for the control and experimental conditions, and Table 10 outlines the stages. In Experiment 1, the experimental condition had a landmark tree to indicate the food location, and the control condition had no landmarks. In Experiment 2, both the experimental condition and control condition had a central landmark between the two hedges. In Experiment 3, there were distal landmarks in the North and South of the arena. In the experimental condition, these remained the same in the transfer test and only the avatar's location changed. In the control condition of Experiment 3, the landmarks in North and South switched to completely novel landmarks in the transfer test.

Trial overview: Trials were self-initiated by subjects by pressing a white square on a blue background. The game consisted of a square arena surrounded by four walls. There were two circular hedges in the centre: one contained four pieces of video game fruit, the other contained a hole. The fruit used was two grapes, and two apples, and subjects were rewarded with a half grape when colleting a video game grape, and a small piece of apple (approx. 1/24th of an apple) for collecting a video game apple (for subject Dorien, the video game apples were rewarded with half a slice of banana as she did not like apples, but these remained visually the same on screen). The hedges were equidistant from the avatar's starting location. Entering the hedge with the fruit enabled the subject to collect this fruit and receive food rewards. Entering the hedge with the hole led to falling down the hole and experiencing a 3-second time out with a blacked-out screen. In some instances, there were also landmarks present (described below). A trial ended either when all pieced of fruit were collected, when a time limit was reached, when the avatar fell down the hole, or when a subject chose to no longer engage with the task. An example trial procedure can be seen in Figures 24-25. Details of landmarks and arenas in each experiment can be found in Appendix B and example starting views of trials can be seen in Figures 22-23.

Exploration stage: Trials began with the avatar in either the North-West, North, North-East, East, South-East, South, South-West, or West of the arena, always facing the centre of the arena. I randomised the starting position for each subject, with each subject experiencing each of the eight possible starting positions once per session (set of eight trials). Fruit was randomly scattered around the arena, but never inside either of the hedges (see Appendix B for details of randomisation). No hole was present in either hedge during this stage. Trials lasted 240 seconds, or ended once all pieces of fruit had been collected. Subjects received two sessions of eight trials. If subjects did not collect all fruit in 6/8 trials in their second session, they were given an additional two sessions, then moved to the next stage regardless of performance. If subjects stopped participating mid-trial, but returned to continue on the same testing day, this trial was paused and re-started. If subjects stopped participating mid-trial and did not return on the same testing day, this trial was re-started on the next testing day that they chose to participate. This stage only occurred in the experimental condition.

Location Learning (visible baiting stage): Trials began with the avatar in the South of the arena, facing North, so that the two hedges were in full view. At the start of each trial, four pieces of fruit could be seen falling into one of the hedges, accompanied by a ‘whoosh’ noise, and four ‘thud’ noises as each fruit landed inside the hedge. Once the fruit had landed inside a hedge, it was no longer visible until the avatar entered that hedge. The hole was in the opposite hedge to the food, and was also not visible. I counterbalanced the baited hedge (West or East) between subjects, and kept this constant for each subject across all experiments and stages. Trials lasted 150 seconds, or until all four pieces of food had been collected, or the hole had been fallen into. If the trial timed out before a hedge had been entered, the trial was repeated. If a subject left the screen before entering a hedge, the trial was re-started when they next chose to participate. If the subject walked beyond the hedges before entering one, the trial was restarted if the subject had not already entered a hedge, or the program moved to the next trial if a hedge had already been entered. Walking into the correct hedge (baited with food) was counted as a correct choice regardless of whether the food was collected. Subjects received six trials per session, and between one and three sessions per day. If subjects stopped participating part-way through a session, they continued that session with no repeated trials on the next day they chose to participate. Subjects passed this stage if they entered the correct hedge in 6/6 trials in one session, or 5/6 trials in two consecutive sessions. If subjects received the maximum number of 10 sessions, they progressed to the next stage, regardless of performance. Details of the number of sessions required by each subject in each stage of location learning (visible, scaffolded, hidden) can be found in Appendix B, Table B3.

Location learning (hidden baiting stage): The procedure and pass criterion for the hidden baiting stage was identical to the visible baiting stage, except that here the food fall routine was not visible. When the food was about to fall into the hedge, the screen faded to black. Once the food had landed in the hedge, the screen returned to gameplay mode with the arena visible. The ‘whoosh’ and ‘thud’ sounds of the food falling were still audible. If subjects received the maximum number of 10 sessions, they progressed through the next stages of the experiment regardless of performance, but their data were not included in the transfer test analyses. In the final experiment (Experiment 3), this maximum was increased to 15 sessions.

Location learning (scaffold): Before moving from the visible baiting stage to the hidden baiting stage, subjects were given a scaffold stage with a combination of trial types from the visible and hidden stages. This stage consisted of eight trials: the first and fifth trials were ‘visible baiting’ trials in which the food falling was seen, and the remaining six trials were ‘hidden baiting’ trials in which the food falling was hidden from view. If subjects stopped participating part-way through a session, they continued that session on the next day they chose to participate, with an additional ‘visible baiting’ trial at the start of that testing day. Subjects passed this stage if they entered the correct hedge in 5/6 of the ‘hidden baiting’ trials in a session. If subjects received the maximum number of 10 sessions, they progressed to the next stage regardless of performance.

Exploration refresher: In the experimental condition, before moving to the transfer test, subjects were given an exploration refresher to remind them of the layout of the environment. This consisted of the 4 trials from their original exploration stage that started in each corner of the arena: North-West, North-East, South-East, and South-West. There was no pass criterion. The trial set-up and procedure were identical to the *Exploration* Stage. This stage only occurred in the experimental condition.

Hidden baiting refresher: This stage was identical to one session of the *Hidden baiting stage*. In the experimental condition, subjects received 6 trials of the hidden stage between their exploration refresher and before moving to the transfer test. The trial set-up and procedure were identical to the *hidden baiting stage*. There was no pass criterion. This stage only occurred in the experimental condition.

Transfer test: The avatar started in the North of the arena, facing South, viewing the hedges (and in some cases, landmarks) from the opposite side to that which they experienced in the location learning stages. Importantly, the hole and fruit appeared in the same hedge as in the training (West or East), but in relation to the subject they had now switched sides. The food fall routine was not visible, as in the hidden baiting stage. The 'whoosh' and 'thud' sounds of the food falling were still audible. The trial procedure was identical to the location learning stages, other than that now the trial would not end or re-start if the subject walked beyond the hedges. This was to allow them to walk to their original starting location and view the hedges from the familiar angle, should they choose that strategy. Subjects received 4 sessions, each consisting of 6 trials across a minimum of 2 testing days. Details of the number of days between exploration stage and transfer test for each subject can be found in Appendix B, Table B4.

Table 10: Overview and number of sessions/pass criteria for each study stage. Asterisks indicate those stages which only appeared in the experimental condition. Stages without asterisks appeared in both the experimental and control conditions.

Stage	**Overview**	**No. sessions / pass criteria**
*Exploration	8 pieces of fruit, randomly scattered around the arena. No fruit in hedges, and no hole. Avatar starts in the North-West, North, North-East, East, South-East, South, South-West, or West.	Session = 8 trials. 2 sessions (if all fruit was collected in 6/8 trials of second session). 4 sessions (if not all fruit collected in 6/8 trials of second session).
Location learning: visible	Fruit is seen falling into one hedge, accompanied by sounds. Avatar starts in the South.	Session = 6 trials. 6/6 trials correct, or 5/6 trials correct in two consecutive sessions Max. 10 sessions.
Location learning: scaffold	Fruit is seen falling into one hedge in trials 1 and 5, baiting is hidden in other trials. All trials are accompanied by sounds. Avatar starts in the South.	Session = 8 trials (2 visible, 6 hidden) 5/6 hidden trials correct. Max. 10 sessions.
Location learning: hidden	Fruit falls into one hedge, always hidden but accompanied by sounds. Avatar starts in the South.	Session = 6 trials. 6/6 trials correct, or 5/6 trials correct in two consecutive sessions. Max. 10 sessions.
*Exploration refresher	8 pieces of fruit, randomly scattered around the arena. No fruit in hedges, and no hole. Avatar starts in the North-West, North-East, South-East, or South-West.	Session = 4 trials. One session.
*Hidden baiting refresher	Fruit falls into one hedge, always hidden but accompanied by sounds. Avatar starts in the South.	Session = 6 trials. One session.
Transfer test	Fruit falls into one hedge, always hidden but accompanied by sounds. Avatar starts in the North.	Session = 6 trials. Four sessions.

Side preferences: Subjects' side preferences were considered when counterbalancing the West and East hedge. For some subjects, data from prior experiments in the virtual environment game were used, and for those who had not completed this previous virtual environment experiment, a side preference test was administered. This was made up of 24 trials with one piece of food presented on the left, and one on the right, within a simple arena with no landmarks. Both pieces of food were equidistant from the avatar’s starting location and were identical to one another in each trial, and varied between trials. Subject Frek received 32 trials and subject Velu received 54 trials due to experimental error. I then assigned subjects as having either a left- or right-side bias, or no side bias. I balanced the number of subjects with left- and right-side biases between West and East hedge groups. Details of side preferences can be found in Appendix B, Table B2.

Hedge training: Three subjects (Kilimi, Tai, and Qafzeh) did not readily enter the hedges once the food had fallen into them and was out of sight. For these subjects, I developed a hedge training intervention. In this stage, the subject started on one side of the arena, facing the hedges from such an angle that one hedge was blocked by the other, creating the image that there was only one hedge, to be approached head on. This was to ensure this intervention did not induce any side biases or affect their later training. No landmarks were present. Once the fruit had fallen into the hedge (as in the visible location learning), I moved the avatar right up to the hedge to a point at which you could slightly see the fruit through the leaves. Then, the subject was tasked with walking the rest of the way into the hedge to collect the fruit. Subject received 6 trials with this help. If subjects walked beyond the hedge, the trial was re-started to avoid any experience with the other hedge. If subjects collected the fruit in these 6 trials, I stopped helping at the start of the trial and subjects had to walk the avatar into the hedge. If subjects still did not walk up to the hedge, I helped again. The pass criterion was a block of 6 trials in which the subject walked into the hedge with no help (or 5/6 in two consecutive blocks). Kilimi received 6 trials with help and 6 without, Qafzeh received 6 trials with help and 12 without, and Tai received 6 trials with help and 12 without. Kilimi moved to this intervention after 10 test days of the visible location learning, Tai and Qafzeh moved to this intervention after 3 test days of the visible location learning.

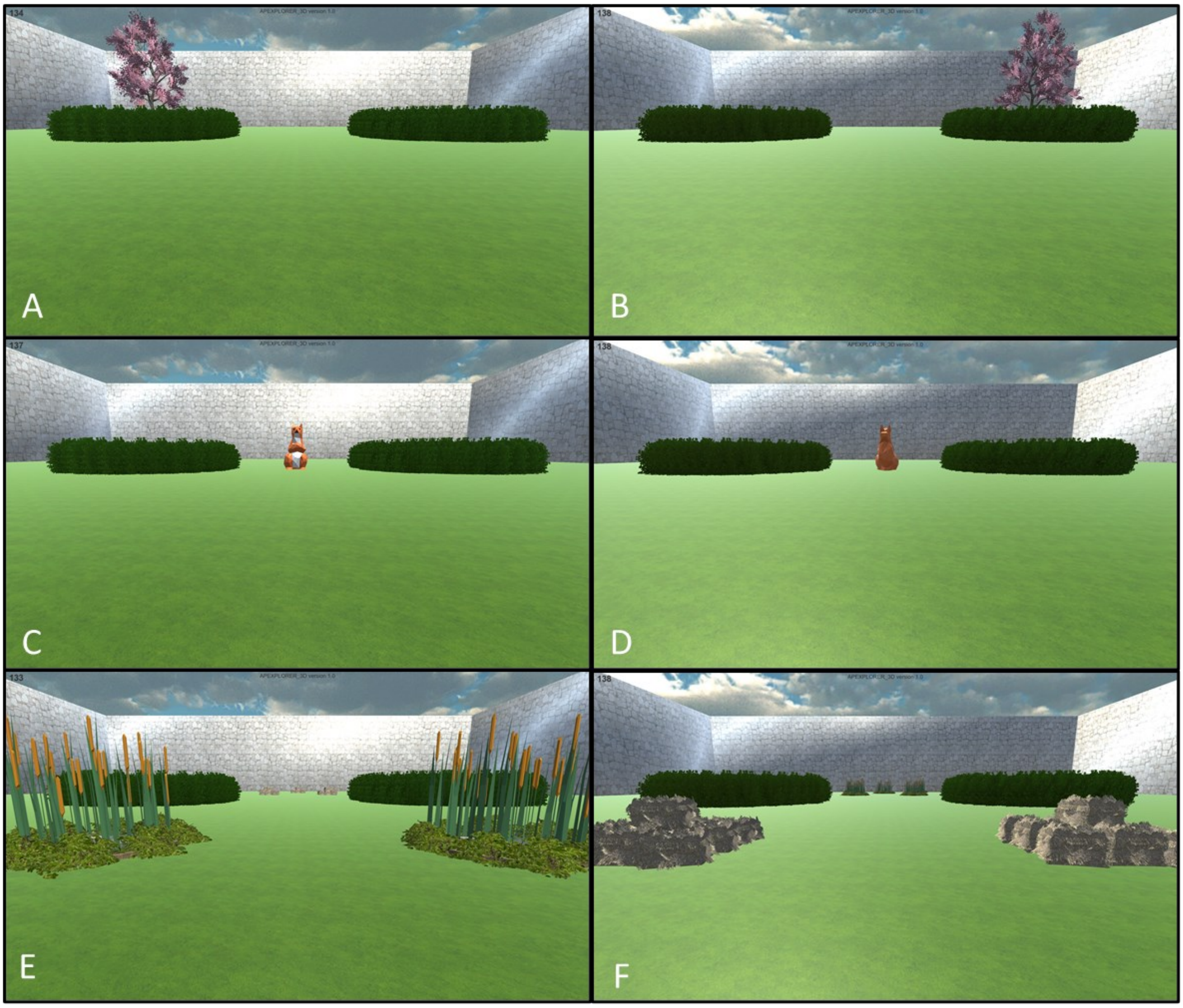

Figure 22: Starting view of trials in the experimental condition of the following stages: A: Learning stages, experiment 1; B: Transfer test, experiment 1; C: Learning stages, experiment 2; D: Transfer test, experiment 2; E: Learning stages, experiment 3, F: Transfer test, experiment 3. Note that the field arena is used in this example, but for half the subjects their experimental condition took place in the beach arena. For these subjects, their experimental condition learning stages and transfer test in experiment 2 resembled C and D in figure 23 below, and their learning stage in experiment 3 resembled E in figure 23 below.

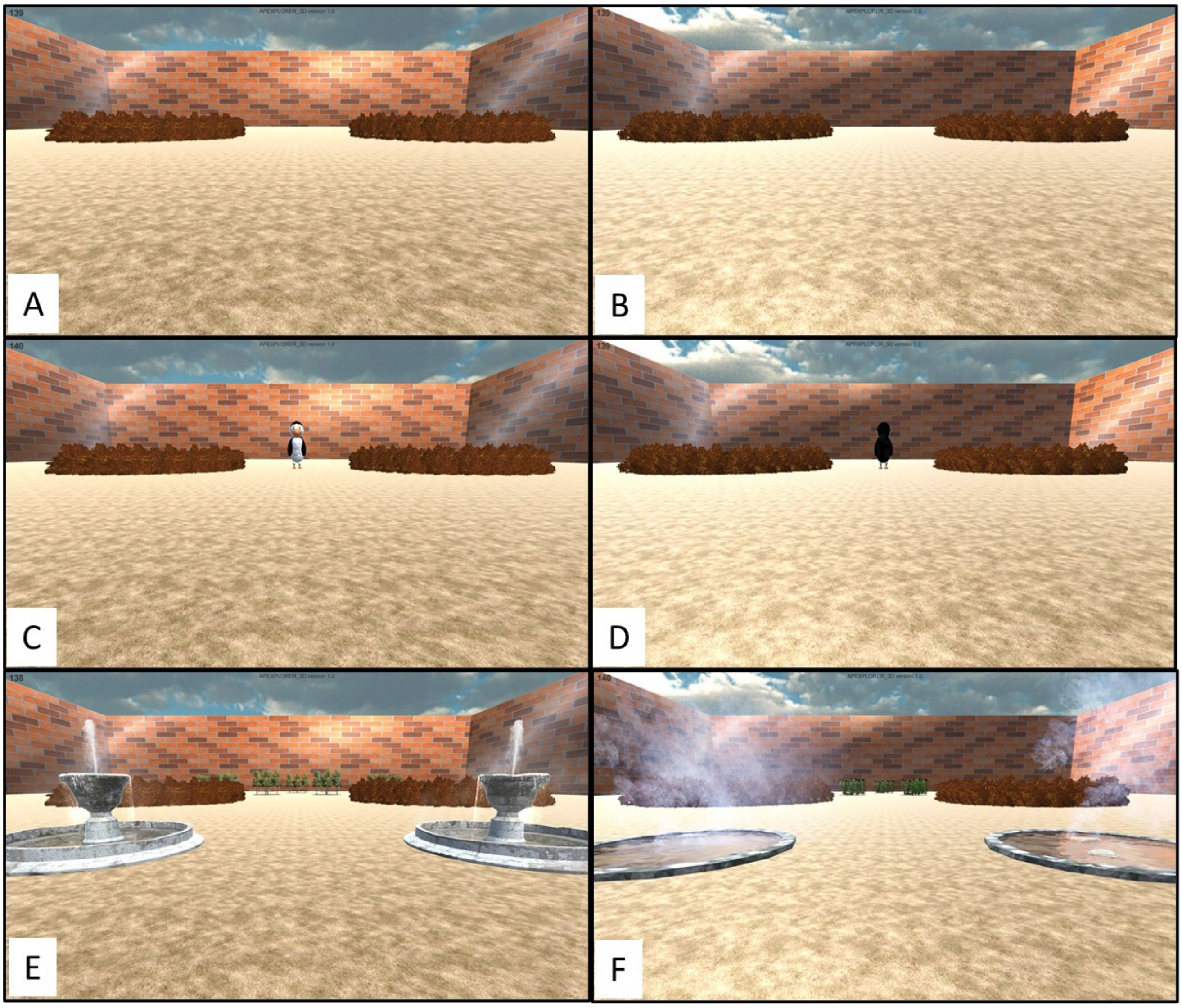

Figure 23: Starting view of trials in the control condition of the following stages: A: Learning stages, experiment 1; B: Transfer test, experiment 1; C: Learning stages, experiment 2; D: Transfer test, experiment 2; E: Learning stages, experiment 3, F: Transfer test, experiment 3. Note that the field arena is used in this example, but for half the subjects their experimental condition took place in the beach arena. For these subjects, their experimental condition learning stages and transfer test in experiment 2 resembled C and D in figure 24 above, and their learning stage in experiment 3 resembled E in figure 24 above.

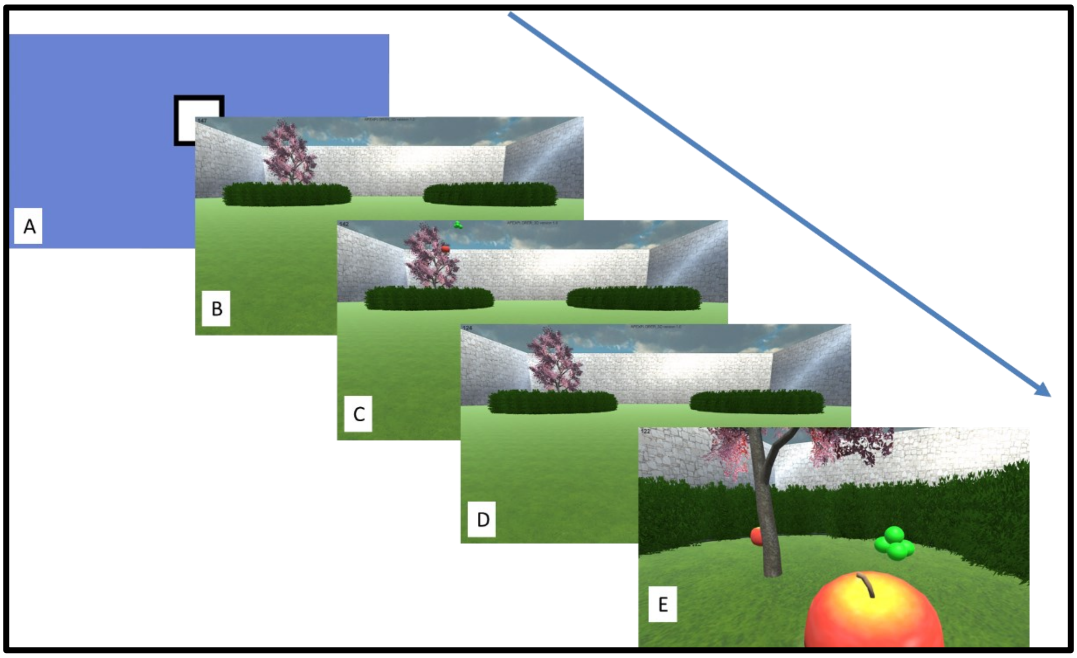

Figure 24: Trial procedure for a visible learning trial. This example uses an experimental trial in experiment 1, in the grassy arena, with the landmark tree and food located in the West hedge. Blue arrow indicates time. A: initiation screen, B: view of the arena at the start of the trial, C: fruit falling into the hedge, D: Once the fruit has landed in the hedge, gameplay begins, E: Avatar walked in correct hedge, about to collect an apple.

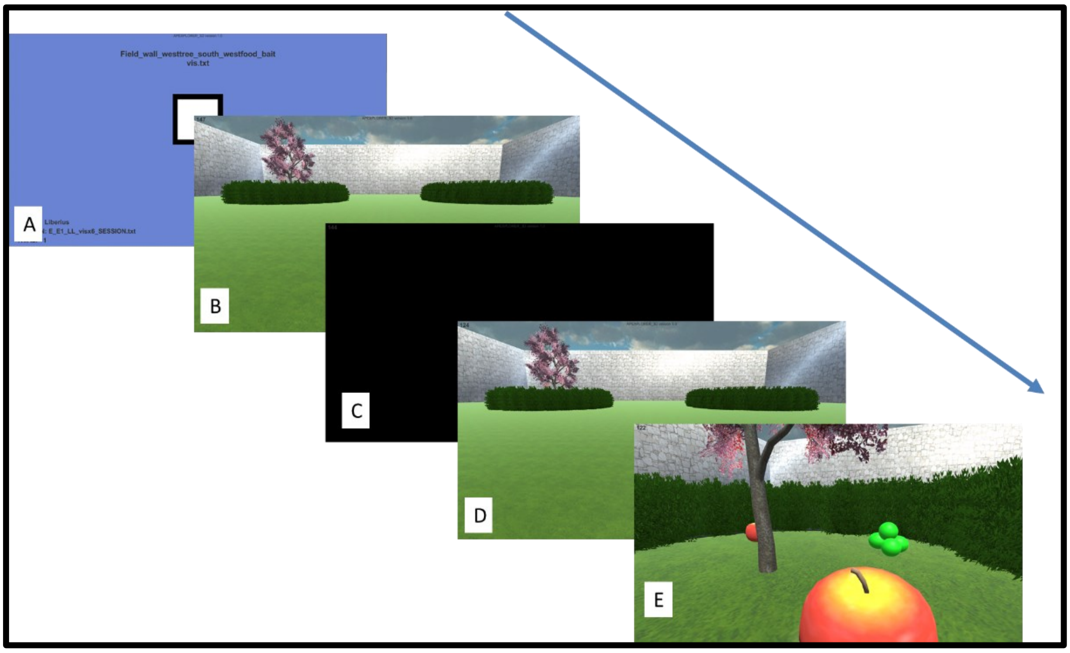

Figure 25: Trial procedure for a hidden learning trial. This is identical to the trial procedure in figure 24 other than panel C which shows the screen faded to black when the fruit falls into the hedge.

An example video can be found for thus experiment via the following link:

https://osf.io/ynvmt/?view_only=ef486ff7178f4d9c8e82f7fc782c17a0

Data Processing

The ApExplorer program recorded any entries into either hedge, and I extracted these data from eventlog output files created by the ApExplorer App. Analyses, visualisations, and model formation followed the same procedure as laid out in Chapter 2.

Results

Experiment 1 – location learning

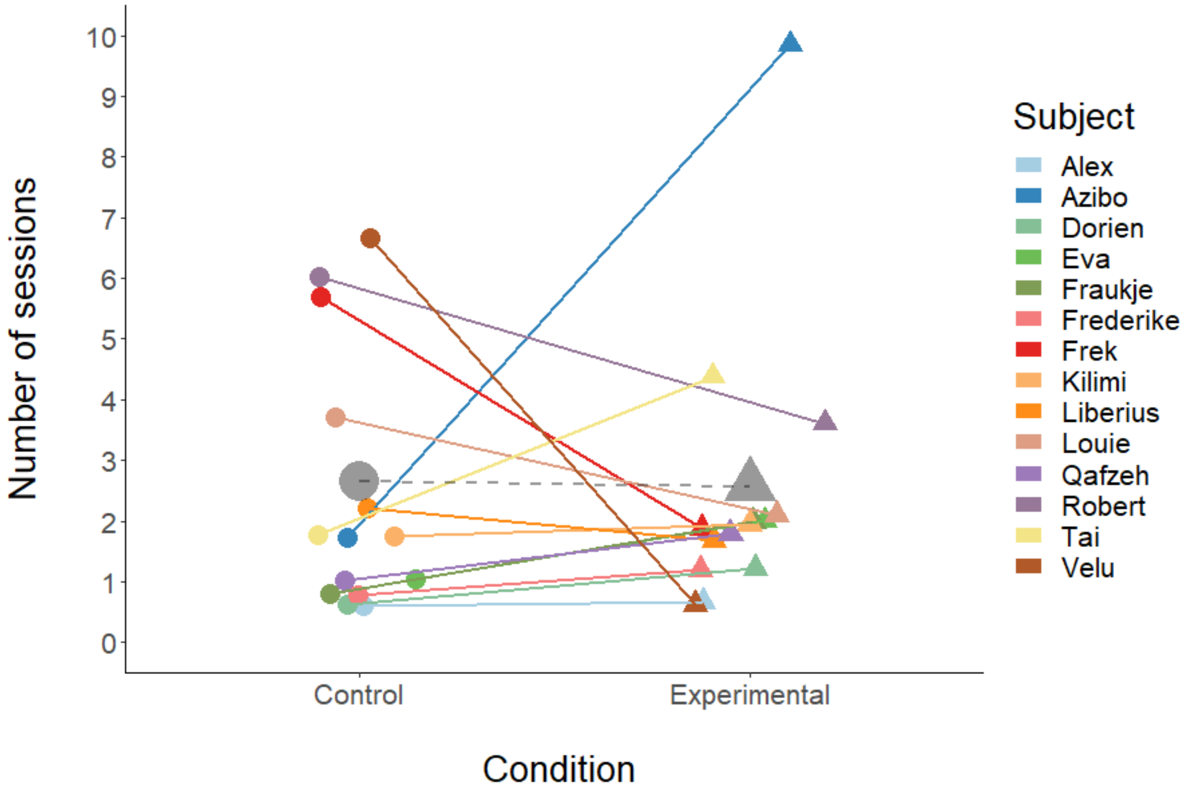

Figure 26: Number of sessions required of the visible location learning stage in Experiment 1. Circles indicate the control condition, triangles indicate the experimental condition. Grey points and dashed lines indicate group means.

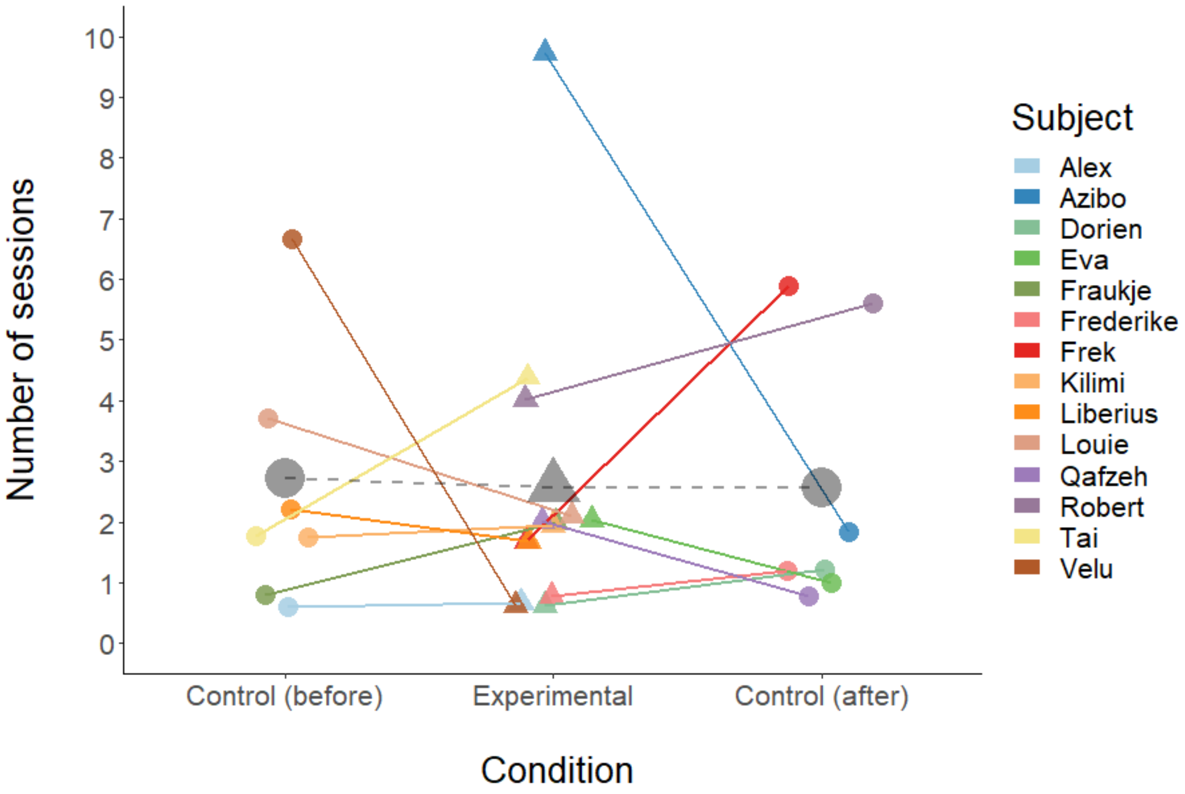

Figure 27: Number of sessions required of the visible location learning stage in Experiment 1, and the order of each condition. Circles indicate the control condition, triangles indicate the experimental condition. Grey points and dashed lines indicate group means.

Location learning: I assessed the number of sessions (blocks of six trials) required by subjects to reach the pass criterion for the visible location learning stage in Experiment 1 in each condition. That is, when learning to travel to one of two hedges, does the presence of a landmark in the correct hedge (experimental condition) facilitate this learning compared to when no landmarks are present (control condition). In cases of repeated stages, the first time the pass criterion was reached is reported. For those subjects who received hedge training, only sessions after the hedge training stage was completed are counted. A Gamma GLMM [Number of sessions ~ Condition + Order + Group + (1|Subject)] revealed no effect of condition (χ2 (1) = 0.29, *p* = .59), no effect of the order of conditions (χ2 (1) = 1.92, *p* = .17), and no effect of group (χ2 (1) = 0.51, *p* = .48) on the number of sessions required. The presence of a landmark did not affect the rate of learning to enter a hedge (Figures 26-27).

Experiment 1 – transfer test performance

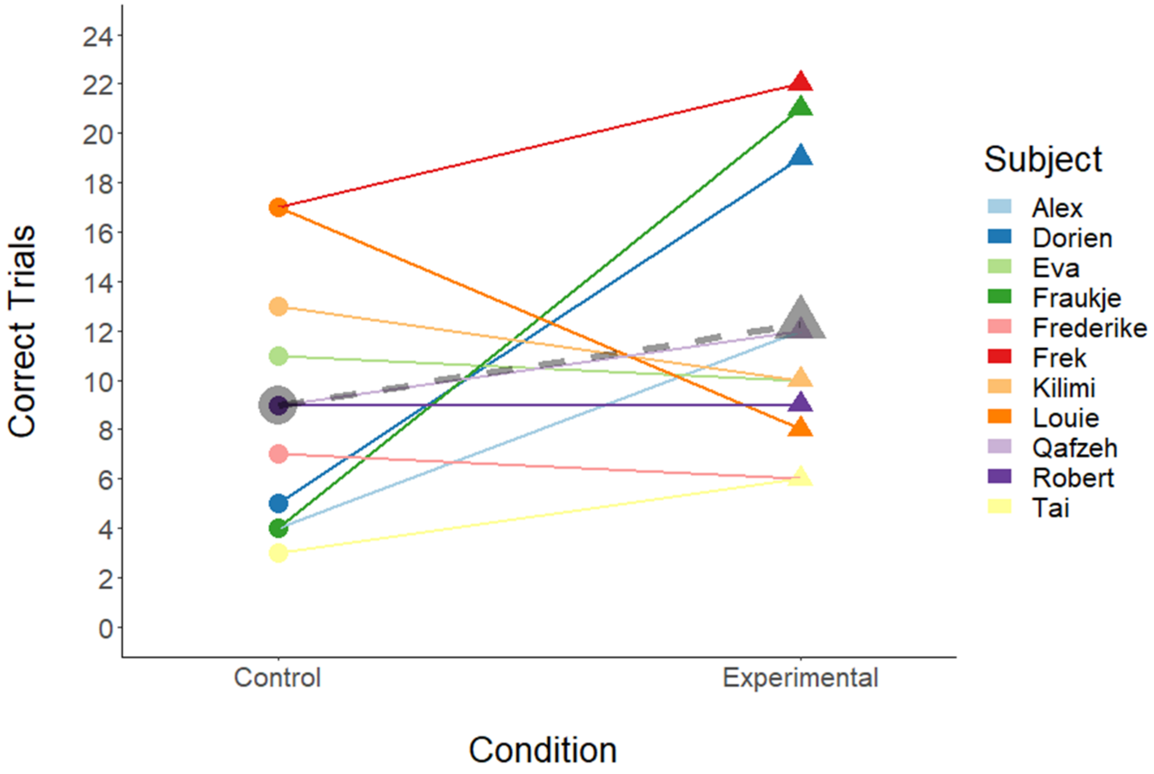

Figure 28: Number of correct trials in the Transfer test in Experiment 1. Circles indicate the control condition, triangles indicate the experimental condition. Grey points and dashed lines indicate group means.

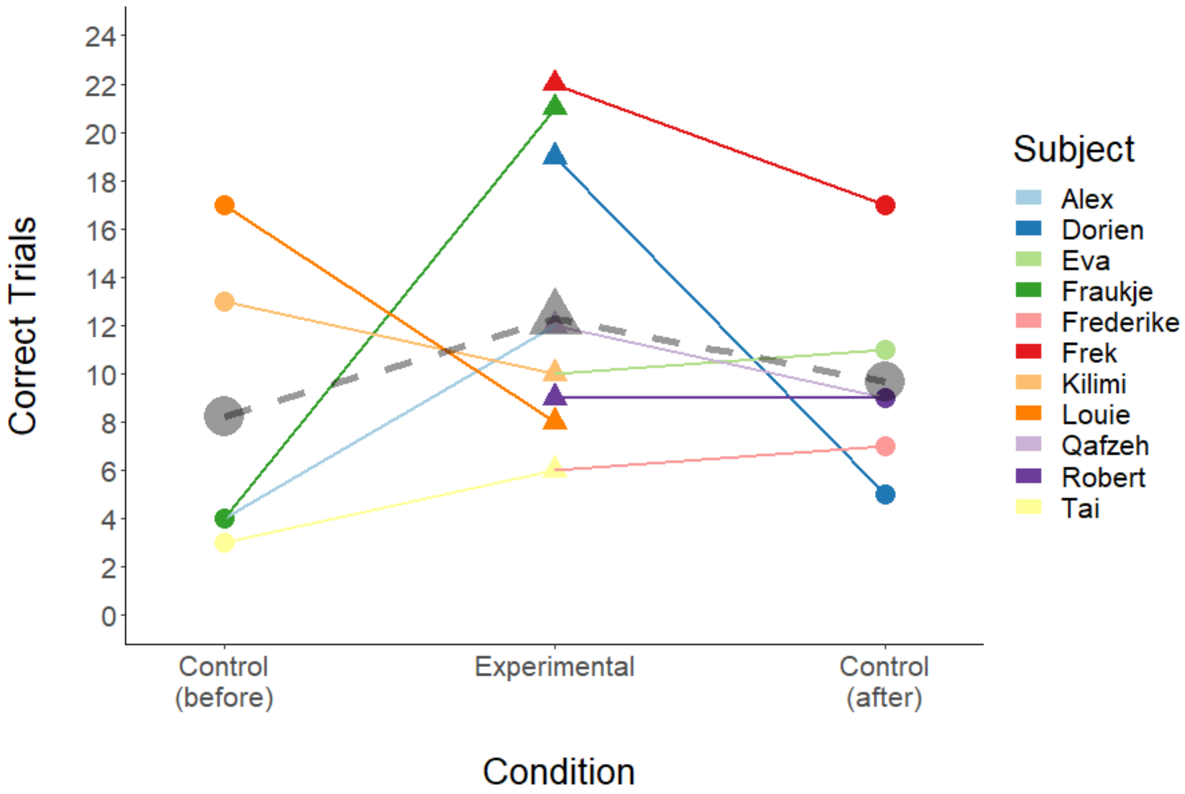

Figure 29: Number of correct trials in the Transfer test in Experiment 1, and the order and which the conditions occurred. Circles indicate the control condition, triangles indicate the experimental condition. Grey points and dashed lines indicate group means.

Transfer test performance: I assessed performance in the transfer test (trials correct/incorrect across 24 trials). A binomial GLMM [Correct/incorrect ~ Condition + Order + Trial + Group + (1|Subject)] showed a significant effect of condition (χ2 (1) = 10.74, *p* = .001, OR = 0.55), no effect of order of conditions (χ2 (1) = 0.01, *p* = .94), no effect of trial (χ2 (1) = 0.97, *p* = .32), and a significant effect of group (χ2 (1) = 4.01, *p* = .045 on transfer test performance (see Figures 28-29). Looking at the overall number of correct trials in each condition, the presence of the landmark improved performance in the transfer test.

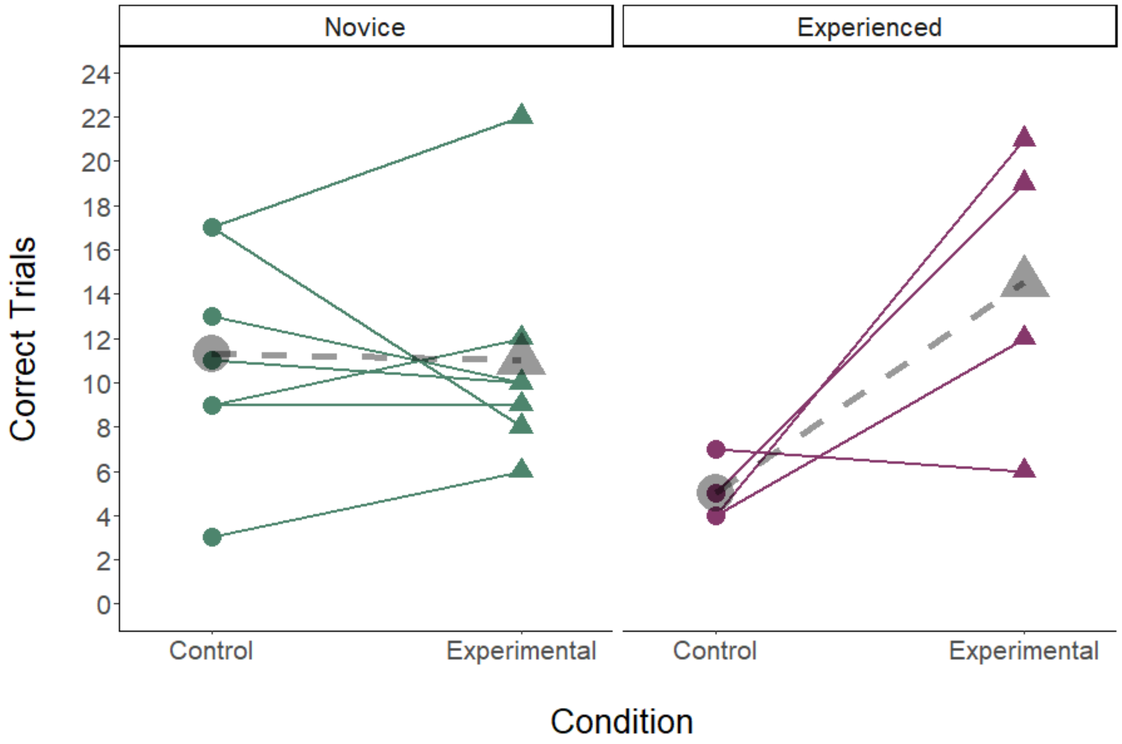

Figure 30: Number of correct trials in the Transfer test in Experiment 1, split by experience of participating in Allritz et al (2022). Circles indicate the control condition, triangles indicate the experimental condition. Grey points and dashed lines indicate group means

Transfer test performance between experienced and novice subjects (exploratory): I conducted an exploratory analysis to investigate the effect of previous virtual landmark experience on transfer test performance. Subjects who were included in Allritz et al. (2022) had previous training approaching a virtual tree landmark to find food which may have enhanced their performance in this study. Group was excluded from this analysis as all subjects who had experience in Allrtiz et al.'s (2022) study were housed in Leipzig. A binomial GLMM [correct/incorrect ~ Experience*Condition + Order + Trial + (1|Subject)] showed a significant interaction between experience and condition (χ2 (1) = 23.46, *p* < .001, OR_{novice} = 1.07, $OR_{experienced}$ = 0.15), no effect of order of conditions (χ2 (1) = 0.24, *p* = .62), and no effect of trial (χ2 (1) = 1.02, *p* = .31). Subjects with prior experience using a virtual tree landmark showed a greater difference between control and experimental conditions (with better performance in the experimental condition) than subjects who did not have this additional experience (Figure 30).

Experiment 2

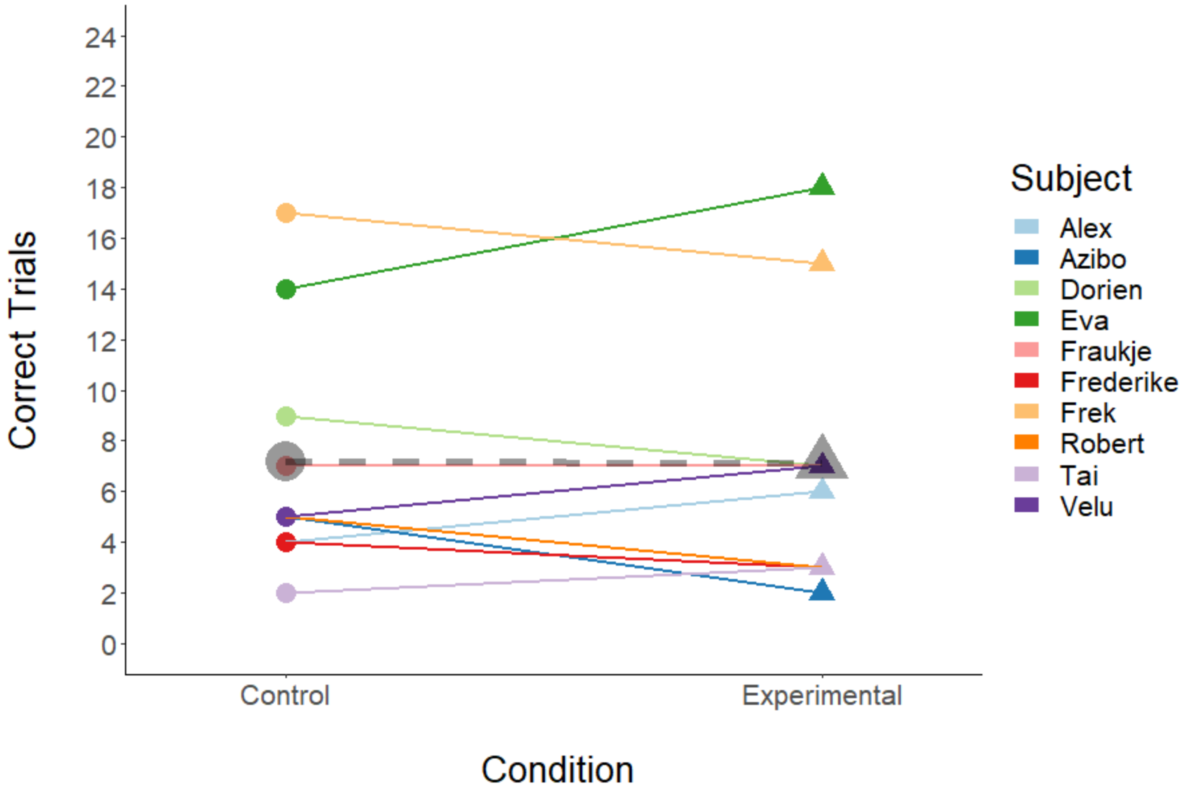

Figure 31: Number of correct trials in the Transfer test in Experiment 2. Circles indicate the control condition, triangles indicate the experimental condition. Grey points and dashed lines indicate group means.

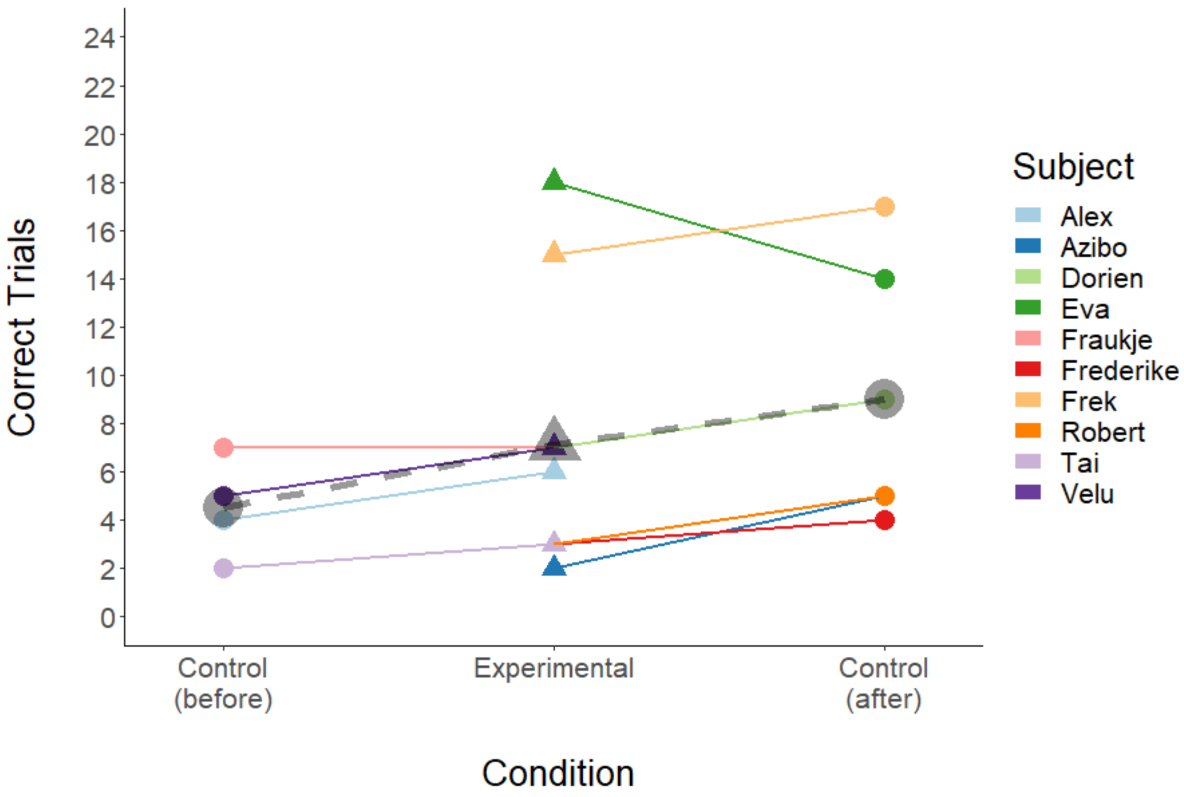

Figure 32: Number of correct trials in the Transfer test in Experiment 2, and the order in which each condition occurred. Circles indicate the control condition, triangles indicate the experimental condition. Grey points and dashed lines indicate group means.

Transfer test performance: I assessed performance in the transfer test (trials correct/incorrect across 24 trials) with a binomial GLMM [Correct/incorrect ~ Condition + Order + Trial + Group + (1|Subject) which showed no effect of Condition (χ2 (1) = 0.04, *p* = .84, OR = 0.96), no effect of Order (χ2 (1) = 1.53, *p* = .22), no effect of Trial (χ2 (1) = 0.60, *p* = .44), and a significant effect of Group (χ2 (1) = 8.63, *p* = .003). Performance was not affected by whether the landmark had been seen from multiple angles, see Figures 31-32.

Experiment 3

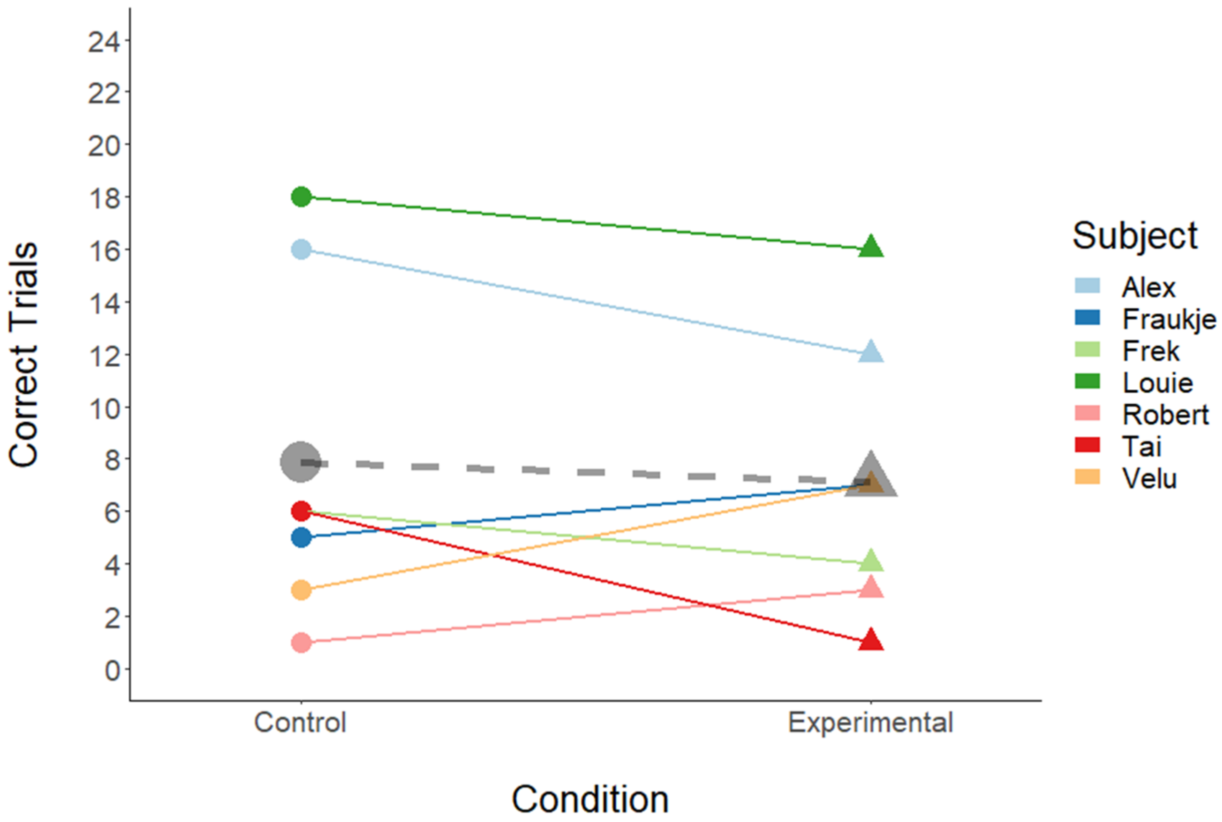

Figure 33: Number of correct trials in the Transfer test in Experiment 3. Circles indicate the control condition, triangles indicate the experimental condition. Grey points and dashed lines indicate group means.

Transfer test performance: I assessed performance in the transfer test (trials correct/incorrect across 24 trials) with a binomial GLMM [Correct/incorrect ~ Condition + Trial + Group + (1|Subject)]. Order was not included due to a very small sample size in one group (only 2 subjects received the experimental condition before the control condition). The model showed no effect of Condition ($\chi2$ (1) = 0.02, *p* = .90, OR = 0.97), Trial ($\chi2$ (1) = 0.06, *p* = .80), or Group ($\chi2$ (1) = 1.10, *p* = .29), see Figure 33. The familiar landmarks did not aid performance in the transfer test compared to novel landmarks.

Discussion

This study presented a virtual translocation task to chimpanzees to assess spatial frames of reference during the navigation of a virtual environment. Experiment 1 revealed a difference in the number of correct trials in the transfer test between the experimental condition with a coincident tree landmark and the control condition with no landmarks. In an exploratory analysis, however, there was an interaction between previous experience and condition. Subjects who had previous experience using a tree landmark to find food (those who had participated in Allritz et al., 2022) showed a larger effect of the landmark on their transfer test performance than those subjects who had not experienced a virtual landmark before. This could indicate that subjects initially use egocentric strategies of going to their left or right, and only with greater experience with landmarks, or specific experience of approaching a landmark from multiple angles, learn to use allocentric strategies. It may be that it was not clear to naïve subjects that the tree was an informative feature in their search for food. In contrast, subjects with prior experience more readily used allocentric strategies. It is difficult to elucidate whether increased experience with a tree-reward contingency helped experienced subjects, or whether it is important to experience approaching a landmark from multiple angles in order to encode it and use it for allocentric navigation.

In Experiment 2, no overall difference was found between the number of correct trials in the transfer test between a condition in which a proximal non-coincident landmark had been viewed from multiple angles and a condition in which it had only been seen front-on. The additional exploration experience of seeing the landmark did not help chimpanzees to later encode the landmark as an allocentric cue. Although, it could be that in both conditions, some subjects were able to use a similar strategy and infer that they were behind the landmark. Nonetheless, many subject performed rather poorly in both conditions and perhaps were relying on egocentric strategies.

In Experiment 3, no difference was found between conditions with familiar or novel landmarks in the transfer test. It may be that these distal landmarks were too far removed from the goal location to be encoded during the learning experiences. Alternatively, by this stage in the series of experiments, chimpanzees may have become reliant on a simple rule of changing their response when the aspects of the environment change, which could be applied equally well in both the experimental and control conditions. These results are difficult to interpret, and further research is needed to make conclusions about frames of reference during large-scale navigation in chimpanzees.

An additional interesting finding in this study comes from the readiness with which many subjects learned to enter the hedges when the food was out of sight, possibly displaying a form of object permanence within the virtual world. Only three subjects required additional scaffolding to walk inside the hedges to find the food, whilst the other eleven achieved this spontaneously. Object permanence, the knowledge that objects continue to exist once they are out of sight, does not appear to be present from birth in humans, but develops in infancy (Piaget, 1954; Baillargeon et al., 1985). It has been demonstrated in several species, including birds and primates (Eurasian jays : Zucca et al. (2007); grey parrots: Pepperberg et al. (1997); rhesus macaques: Wise et al. (1974); squirrel monkeys: Vaughter et al. (1972); orangutans: de Blois et al. (1998); chimpanzees: Wood et al. (1980)). While it has been shown that infants are able to translate this ability to two-dimensional animated displays on a screen (Durand & Lécuyer, 2002), to my knowledge the object permanence ability of chimpanzees with virtual stimuli has only been tested with two subjects (Beran & Minahan, 2000), (see also Péter et al. (2011) for some promising findings with dogs at least when they could respond with no delay). While it cannot be concluded that object permanence explains the chimpanzee's behaviour here, and not more simple location cueing based on the last place food was visible on the screen as it entered the hedge, the impressive speed with which most subjects passed this test warrants further investigation.

There are a number of possible reasons for the lack of differences observed between experimental and control conditions which will now be discussed. These relate to the nature of the training and stimuli, the cognitive flexibility demands, and the virtual environment method more broadly. Firstly, the landmarks may not have been salient enough for subjects to use them as cues to aid their search. In Experiments 2 and 3, as the landmarks were not coincident, subjects could have easily not attended to them at all during the location learning. Moreover, the central landmark used in Experiment 2 resembled a social agent (i.e., a squirrel or a puffin). If these were represented as social by subjects, these would not be considered reliable landmarks. Viewing social stimuli from a different angle does not necessarily indicate a change in location, rather, it could be that the agent has turned themselves around. It is also possible that during the exploration stages, subjects may have been solely focused on the food in the environment. This could have led to 'tunnel-vision' attention and prevented attention being drawn to anything else in the space. Future work could use eye-tracking as a manipulation check, to see whether apes attend to the landmarks at all when viewing the virtual arena (a method previously successfully used with great apes, for example, Krupenye et al., 2016) as it is not clear from this experiment alone what environmental features were attended to or encoded.

No effect of trial was seen in the transfer tests, suggesting that the initial reward contingency that had been learned was difficult to extinguish, and improvement was not seen across 24 trials. It may be that a relatively low-effort behavioural response of touching a conditioned stimulus may be difficult to inhibit after extensive training. Moreover, the visible location learning always took place from the Southern viewpoint, and so the food was only ever seen with the hedge from this angle. It may be that experiencing seeing the food in the target location is important for spatial encoding or that the memory of seeing the food in that screen location was a factor in how the subjects chose to search. Other paradigms could glean more about chimpanzees' use of landmarks in virtual environments without requiring a repeated behaviour. For example, an observation-only learning condition, with only the test condition requiring a behavioural response could investigate which allocentric cues can be used as referent points (similar to the method used in Kuhlmeier & Boysen, 2001). However, some other research suggests that we learn better by doing an action ourselves than simply observing it, so there are costs and benefits to consider with both methods (Gerson et al., 2015).

Whilst some subjects performed well in both conditions of the transfer tests, others performed somewhat poorly and showed perseverative behaviour rather than switching their responses after negative feedback. It may be possible that the nature of the location learning led to automatic behaviour in some subjects. Theories of associative learning would suggest that when a stimulus becomes strongly associated with a reward (becomes a conditioned stimulus), the very presence of that stimulus can elicit a response associated with obtaining that reward (conditioned response), (Pearce, 2014). Subjects received several learning trials in which touching one of the hedges moved their avatar towards the food, and subsequently led to obtaining a food reward. It may be that, as there were so many learning trials, this behaviour at some point became more automatic than thoughtful and the mere sight of the hedge on the left or right of the screen elicited the response of touching it, without attention being paid to any other aspect of the environment. This may especially be the case as the exact action sequence (reaching and touching the same side of the screen on each trial) did not have to change during learning trials and may have become rote. It could also be the case that the association with the hedge blocked any other associations forming between landmarks and reward. Indeed, in humans, only aspects of an environment which are considered necessary to locate a target are encoded and often other aspects of a search space are ignored or not remembered during memory retrieval (Ho et al., 2022). In movement ecology, it has been suggested that there may be a trade-off between spatial memory ability and cognitive flexibility, so the two skills may oppose one another (Tello-Ramos et al., 2019). That is, a strongly retained memory for a location may interfere with the acquisition of new information, which may explain some subjects' poor performance in the transfer tests.

As discussed previously, this experiment also serves as a test of reversal learning abilities, assessing cognitive flexibility. If the strategy learnt during training is an egocentric one of choosing the hedge to one's left or right, then the correct response in the transfer test is a reversal of this contingency as the correct hedge now appears on the opposite side of the screen. While some studies report successful cognitive flexibility with chimpanzees (for example, Cantwell et al., 2022), there are also cases in which behavioural conservatism is reported in primates, especially when tasks are challenging (for example, chimpanzees: Davis et al., 2019; monkeys: Whitham & Washburn, 2020). Particularly in spatial reversal, a relation between cognitive flexibility and age has been reported (dogs: Christie et al., (2005); monkeys: Lai et al., (1995); Bartus et al., (1979); apes: Manrique & Call, (2015)).

Most studies reporting a decline in performance as animals get older (although a U-shaped relationship was found in Manrique & Call (2015), with both younger and older subjects showing more perseverative responding). Cantwell et al., (2022) found that chimpanzees were better at switching when the initial learning condition required the use of spatial cues than the use of perceptual cues, which the authors conclude suggests that chimpanzees preferentially use spatial information (i.e., left and right). The opposite interpretation could also be made here that, as reversal learning was harder after learning with a perceptual cue, this association was stronger and harder to shift from. To put the present study into this context, some subjects switched their responding more easily when a combination of spatial and perceptual cues were available during the learning stage (Experiment 1, experimental condition) than when only spatial cues were available (Experiment 1, control condition). This suggests that learning the opposite contingency to the learning stage was harder when only spatial (left/right) information was available, and was aided by the presence of a perceptual cue/landmark; a similar finding to Cantwell et al. (2022), although a slightly different interpretation of the results.

Individual differences in overall reversal learning/switching ability were observed, with some subjects showing lots of perseverative behaviour, and others showing reasonable success in the transfer tests. As no difference in overall number of correct responses was found between conditions in several subjects across the series of experiments, individual cognitive flexibility may explain the results better than frames of reference or landmark use. Further research with a larger sample size could probe this further.

Alternative factors may have influenced task performance here, such as unintentional effects from extraneous cues. In Potì's (2000) rotational task with capuchins, the author notes that 180° rotation was the most challenging, as the stimuli presentation was very similar before and after the rotation. This led capuchins to be more likely to adopt an egocentric search strategy in these rotations. It may be that the nature of the rotation we chose in the present study was the most challenging form, and starting with smaller rotations between learning and transfer stages may yield different results. Potì also noted that subjects in their task may have relied on external cues in the room, suggesting the scale used by monkeys to search for the target was not limited to the table on which the stimuli were presented. A similar strategy has also been reported with great apes (Hribar et al., 2011). It is difficult to rule out in our task whether subjects limited their search cues to what was presented on the screen, or whether other spatial cues around them could have been encoded during their location learning, such as the edge of the touch-frame, a wall, the experimenter, etc. Such cues remained constant between the location learning and transfer tests, whereas in real-life translocation, the perspective of one's entire environment shifts. It should be mentioned that while subjects in the Leipzig group always participated in the same location (for each subject), due to practical demands in Edinburgh, the testing location was not always consistent across sessions (although there are several differences between the two groups' testing environments, so differences between them are difficult to interpret).

In some virtual environment tasks, humans demonstrate the use of geometric information, such as the distance between the start location and target location (Yang et al., 2019), and rats in some cases prefer to use boundary cues over landmark information (Cheng, 1986). If subjects in this study used either of these strategies, their performance in the transfer test could look random as the two hedges were equidistant from the start location and from each wall of the arena. However, using this strategy would make it challenging to reach the pass criterion during the training. It is hard to conclude whether poor performance in the transfer test reflects the use of egocentric processing, or allocentric processing on a different scale.

There are a number of limitations inherent to the virtual environment method. The most obvious difference between moving through a virtual environment and a real-life environment is the lack of proprioceptive feedback when navigating on a screen, which may cause differences between spatial processing across these two domains (Ruddle et al., 1997; Fernandez-Baizan et al., 2019a). Virtual environments in this set-up can only tap into wayfinding abilities without any locomotion cues, which are a key component of real-life navigation, (Montello, 2005). Furthermore. any other sensory modalities which could be used in real-life navigation are also excluded from virtual environment navigation. Additionally, the nature of the translocation in this task was very different to how translocation occurs in reality. In fact, in a virtual environment translocation task with children, van den Brink & Janzen (2013) found that optic flow was more important than object/landmark use from a young age. It may be that, had the apes in this study witnessed the perspective move around to the opposite side of the screen, they may have had more success. This is in line with previous work showing that great apes can track spatial rotations when the rotation is visible, but, despite the presence of some landmarks, struggle to infer the location change when the rotation is unseen (Okamoto-Barth & Call, 2008).

As previously mentioned, there are several environmental cue changes that can be integrated during real-life navigation, and the use of a single cue change here may have been too challenging for subjects. Further, great apes may not apply real-world physics to virtual environments. Subjects were given experience with starting from different locations and angles in different trials during the exploration stage, and during prior virtual environment training. While the aim was to show the environment from several viewpoints to aid in later navigation, this may have unintentionally taught subjects that this environment is changeable and that sometimes landmarks appear another way from trial to trial, making them unreliable cues. While virtual environments are a useful tool in primate cognition, their use is not without limitations. When generalising to navigation more broadly, it should be acknowledged that spatial processing may be more demanding in virtual settings and a poor performance on a virtual task may be a feature of task demands beyond the experimental question. Virtual environments could also be used in conjunction with real-life tasks, and the combination of virtual and physical stimuli, such as augmented reality, could also be further explored (for example, Juan et al., 2014).

Of course, there are many factors aside from landmarks which impact and shape animal movement. Deciding where to move and which visual cues to respond to is only one part of the decisions which affect when and how an animal moves (Nathan et al., 2008). Some groups of animals respond to group-mates' movements, sometimes employing leader-follower roles (Averly et al., 2022; Sasaki et al., 2018; Tokuyama & Furuichi, 2017), or vary their strategies based on food scarcity (Presotto & Izar, 2010). Chimpanzees also engage in group travel (Gruber & Zuberbühler, 2013), so spatial cognition within a social context may look different to solo navigation. Responding to social cues may be more important than to environmental cues, especially to certain individuals who are less likely to lead the group movement, as in some species more dominant or more bold individuals are more likely to lead than to follow (Sasaki et al., 2018; Tokuyama & Furuichi, 2017). Chimpanzees tend to have hostile interactions with out-group members (Wrangham, 1999; Williams et al., 2004), and so bearing in mind the location of other groups and staying within their own home-range may also be important considerations; being aware of predators, out-group members, or potential prey may guide movement decisions in animals more so than landmarks. That being said, chimpanzees have demonstrated knowledge of their environments in field studies (Janmaat et al., 2013) and it is likely that, like humans, some individuals respond to spatial cues. It may be that in this study, the cues chosen as landmarks were too different to cues used in real-life navigation, for example, some groups of humans also rely on the position of the sun to help with wayfinding (Jang et al., 2019). Future work could consider other visual cues that could be employed in virtual environment navigation, as well as whether social cues are important too.

In sum, a subset of chimpanzees in this study was able to use a single, coincident landmark as a beacon to find food in a virtual environment. Success in this task interacted with prior experience of using a virtual landmark, which possibly indicates that the type of experience with a landmark is important for spatial encoding. Exposure to different approach angles could influence spatial frames of reference or landmark use. In the second and third experiments, chimpanzees as a group did not appear to benefit from the presence of a central landmark or distal landmarks when approaching the goal and distractor locations from the opposite side to their training. Possibly, apes can recognise landmarks and associate them with food locations, but do not integrate directional information about landmarks. Constraints on cognitive flexibility, salience of cues, and repeated movement during training may have hindered subjects in this task, and thus it is difficult to make clear conclusions about chimpanzees' spatial frames of reference in virtual environments. In some cases, though, it seems that chimpanzees may rely on egocentric encoding and more research is needed to investigate whether chimpanzees may switch between strategies and what environmental factors contribute to this.

Chapter 6: General Discussion

6.1 Summary

The work presented in this thesis contributes to the growing body of evidence that chimpanzees are capable of "actively coordinated collaboration" (Duguid & Melis, 2020). That is, when working jointly with a partner, chimpanzees consider the actions of their partner rather than only their own role. In Chapter 2, I showed that chimpanzees passed a tool to a human partner in a manner which accommodated the partner's action constraints and ease. In Chapter 3, I demonstrated subtle differences in action learning after a co-operative interaction compared to a non-social learning context, showing evidence of role-reversal in a joint action task. In Chapter 4, I aimed to develop a task that would assess co-representation via co-efficiency considerations, but instead found that in some cases chimpanzees do not have preferences to minimise effort. This will be useful for future work in showing that efficiency or effort preferences cannot be assumed, and other paradigms should be explored. For Chapter 5, I co-developed a virtual environment software for the use of primate cognition research broadly. I aimed to probe frames of reference use in chimpanzee navigation of virtual environments as a starting point for validating this measure for future work, and offering a first step towards developing social tasks in virtual settings such as perspective-taking. This could provide a steppingstone towards virtual cooperative games for great apes. In this final chapter, I will summarise my findings and reflections on the topics of joint action and virtual environment navigation. I will also offer thoughts about the limitations of this body of work and considerations for future directions.

In Chapter 2, I presented an object passing task to chimpanzees. To extract food rewards from an apparatus, I needed chimpanzee subjects to pass me a tool through a testing window. I manipulated my hand position, ease of access, and action capability and found that these factors influenced the location in which chimpanzees passed me the tool. Across six experiments, chimpanzees passed the tool in a way that accommodated my action capabilities and ease. In order to accommodate my action, chimpanzees had to consider my action possibilities and make predictions about my actions to incorporate them into their internal action models. If they had only considered their own task of transporting the tool to the experimenter side of the testing window, their passing locations may not have been influenced by factors affecting my action. Returning to Duguid and Melis's (2020) definitions for collaboration, these findings are indicative of actively coordinated collaboration as they demonstrate chimpanzees' knowledge of a partner's actions.

The findings from Chapter 2 would be strengthened with the inclusion of a non-social control, as it cannot yet be ruled out that more simple strategies may have been adopted by subjects, for example, avoiding barriers. Likewise, the findings could reflect individual action plans such as getting the tool to the experimenter's hand, with the same motor plan as if they were independently placing the tool into a target location. To understand whether this behaviour truly shows a consideration of a partner's actions, non-social controls should be investigated, as well as the flexibility of this behaviour. For example, looking at whether chimpanzees wait for an experimenter to be ready to receive a tool if they are otherwise occupied, or adapt the orientation of an object during a handover. Nonetheless, this study, which took inspiration from human joint action literature (Meyer et al., 2016; Constable et al., 2016), was easily adapted for use with primates, and could be easily implemented in many settings with diverse species.

Chapter 3 looked at action learning a in partial role-reversal task. Chimpanzees learnt the second action in a two-action sequence, in either a cooperative condition (that is, with a human experimenter performing the first action) or in a non-social control condition (in which the first action occurred via an object falling). In a test phase in which chimpanzees now had access to perform the first action, and the human or object did not perform their role, I assessed chimpanzees' ability to execute the first action between the two conditions. Whilst previous experiments show few differences in action learning between chimpanzees with no experience in a cooperative task compared to chimpanzees reversing roles in a cooperative task (Fletcher et al., 2012), in this task we found subtle differences between groups. Although the overall number of successes and latencies to succeed did not differ between groups, I observed differences in solution style. The group who had experienced the cooperative task with a human experimenter solved the task in the expected way, acting on the apparatus in a similar way to the experimenter and doing so consistently after solving the task. In contrast, the group who had learnt in the non-social condition solved the task in more unexpected, novel ways, and did so less consistently. This may indicate that chimpanzees in the non-social group may have had a less clear understanding of the action and may have learnt through emulation or bootstrapping the end-state of the apparatus. This supports the notion that chimpanzees co-represent joint tasks and supports the hypothesis that chimpanzees engage in Duguid and Melis' (2020) actively coordinated collaboration.

I also assessed the number of times subjects left the testing area in Chapter 3, and their latencies to do so. I hypothesised that those in the cooperative condition may have a stronger sense of joint commitment, or a greater expectancy of action from the experimenter, but no evidence was found in support of this. An additional consideration here could be coding communication attempts from the subject to the experimenter, as increased communication or reengagement efforts in the cooperative condition could indicate a greater expectation of the experimenter to perform their role and offer evidence of a sense of a shared commitment. This experiment offers a new testing paradigm which chimpanzees took to with relative ease, and which could be adapted to other primate species and other topics of study. Moreover, this study has highlighted the importance of considering the qualitative differences when coding behaviours, as simply counting the overall occurrences can sometimes mean missing critical behavioural patterns. Future research should continue to assess subtle, as well as more obvious, differences in behaviour. Such research could borrow methodologies from other fields, such as the Levenshtein distance used in human-robot interaction research (and originally borrowed from the field of biology, used for DNA sequence analysis, and in linguistics), which can be used to assess the number of differences between two action sequences (Hauge et al., 2021).This study, in particular, suffered from a small sample size, as the design required a between-subjects sample. As only a subset of the small sample solved the task in the test phase, concluding that their differences in style and consistency in solving the task is due to their different learning conditions may be premature, and individual differences driving these responses cannot be ruled out.

In Chapter 4, I was interested in humans' seemingly unique social motivation (Tomasello, 2014). Despite lots of evidence that chimpanzees are capable of working together (outlined in the General Introduction, Chapter 1), when given the option, they prefer working alone, unless collaborating leads to a higher pay-off (Bullinger et al., 2011a; Rekers et al., 2011; Bullinger et al., 2011b). This raises the question of what motivates this preference. Rekers et al. (2011) note that, despite chimpanzees needing significantly more time to obtain a reward alone than with a partner, working alone was still their preferred option. Another approach is to manipulate the amount of physical effort needed to complete a task, and ask whether this affects chimpanzees' likelihood of sharing a task. I aimed to develop a paradigm in which chimpanzees would be motivated to minimise their action effort to look at the impact of this on the likelihood of choosing a collaborative option. Such a paradigm could be used to study co-efficiency and understand more about how chimpanzees may co-represent joint tasks (Török et al., 2019; Strachan & Török, 2020). Chimpanzees in this task were not motivated to minimise their effort with the puzzle box task I created, and often continued acting on the same side rather than switching their location to access the easiest of two options. Most chimpanzees became flexible in their responses once one option was made impossible, and now selected the only box from which they could gain a reward. After the experience with the impossible box, subjects returned to their lack of preference or side biases, and once again showed no preference between a high and low effort option. The performance with the impossible condition suggests that, at least for those subjects who performed well in that stage, lack of flexibility or task understanding did not explain the pattern of results. Rather, it may have been that the box was enjoyable to use or that chimpanzees in this captive setting did not feel the need to reduce their physical effort. It is possible that an additional time pressure such as a competitor or a reward which has a time limit (such as melting) could induce a preference. From this study, we can learn that we should not assume that chimpanzees will seek the easy route in tasks, and a different paradigm would be required to assess co-efficiency.

For Chapter 5, I co-developed a new software for studying primate cognition (Schweller et al., 2022) and used this to study spatial frames of reference. After learning to travel to a goal location in favour of a distractor location from the South of an arena, subjects were faced with a translocation task in which they began trials from the opposite viewpoint in the North. Using varying virtual landmarks, I found differences in overall number of correct responses when a landmark was present compared to no landmarks, suggesting by this metric that subjects were using allocentric encoding (Experiment 1). However, subjects who had previous experience with a similar virtual landmark used a landmark strategy more readily in this task than novice subjects. This would suggest that a landmark-based navigation strategy may only appear once landmarks are seen and approached from multiple viewpoints. In Experiment 2, however, a condition with a central proximal landmark that had been seen from multiple angles did not elicit better performance in the translocation test than a condition with a landmark only viewed from the front. Perhaps, experience approaching a landmark from multiple angles is important, and only seeing it from different views is not enough to encode it as a spatial cue.

I also did not find a difference between conditions when using distal landmarks (Experiment 3) that were either familiar or novel. It may be that these cues were too far away from the goal location to be used in wayfinding. Possibly, if subjects had received more trials in the translocation tests, the overall number of correct trials may have differed between conditions as they continued to consistently respond correctly, but this is speculative. The nature of the translocation in this task may have been too dissimilar to real life movement through space, and the training stages may have encouraged perseverative responding in this task. Subjects showed impressive object permanence understanding in the virtual world, and were able to remember a goal location and select it over a distractor location, two results which are encouraging for future work with virtual environments. The subjects struggled with the reversal learning aspect and at times showed limited cognitive flexibility, and future tasks could consider using more trials in reversal learning studies to allow subjects more time to switch their responses.

Moving forward, virtual environment tasks could continue to be developed and this new method could be expanded to study aspects of joint action. For example, pairs of chimpanzees could work together to simulate a monkey hunt, or virtual versions of classic stag-hunt tasks could be implemented. The current study aimed to act as a step towards validating this methodology, examining whether the virtual space is conceived by chimpanzees to be three-dimensional, and whether they could conceivably take the perspective of another agent in the world. This study alone cannot answer these questions, but further work could develop this method further and adapt this paradigm for social tasks to learn more about chimpanzee social and spatial cognition, and the interplay between the two. Studying how animals conceive of their environments and how they find their way is important both for considering how to craft the most appropriate and enriching enclosures in captive settings and for conservation efforts with wild animals (Ogburn et al, 2017; Doherty, 2018; Katzner & Arlettaz, 2020).

Learning more about joint action is crucial for understanding the evolution of human cognition, and some hypotheses of human evolution highlight advances in the social world of early humans when considering the differences in our lineage to other apes (Tomasello et al., 2012). Learning about the socio-cognitive profile of our closest living primate relatives and sketching out the similarities and differences between how humans and apes navigate their social worlds could be a key piece of the puzzle of human evolution. Considering Tinbergen's (1963) questions, as well as the ultimate, phylogenetic goals of this research, there are more proximate goals of understanding mechanistic explanations for animals’ behaviour. Whilst the study of chimpanzees naturally lends itself to questions of evolution given our phylogenetic proximity, understanding chimpanzees' cognitive mechanisms is an important and interesting question in and of itself. Such pursuits can inform welfare of captive primates, such as highlighting their complex sociality and imperative social needs to ensure social housing, as well as shedding light on their general intelligence to possibly encourage conservation and discourage mistreatment.

The focus of research questions with chimpanzees often regards direct comparisons of cognitive abilities between our two species to learn about our own evolution by making inferences about our last common ancestor. While this is an interesting and fruitful scientific approach, it can perhaps at times be beneficial to step away from the phylogenetic tree and instead examine the cognitive mechanism itself. Drawing direct comparisons between chimpanzees and humans, and only asking how they fit into the human cognitive architecture, may ignore the vast differences between our two species. Naturally, when we design experiments, we bring an anthropocentrism; a human bias. While our training and experience with the animals we study, as well as careful thought to eliminate such biases, can go some way to resolving this, it is difficult to extinguish entirely. This may especially be the case when studying social cognition compared to physical cognition, with which we may be able to be more objective when defining variables that are not so latent. It is challenging to target the chimpanzee social landscape when we see it only through the human lens. Might we be only looking for human-like behavioural indicators of sophisticated collaboration, and thus concluding it does not exist in our closest living primate relatives when we do not see it? For example, in the study of chimpanzee communication, when communication is directed towards a human, an enculturated chimpanzee may use a pointing gesture (Call & Tomasello, 1994; Leavens et al., 2019). Pointing is quite clear for us to observe, as it fits into the human communication repertoire. Studying chimpanzee communication between conspecifics can be more challenging and can rely on measuring behaviours that are more subtle to us and require a different framework (Grund et al., 2023). Could this be the case for other aspects of social cognition? Chimpanzees may be capable of more sophisticated joint action mechanisms, such as shared intentionality, but the behavioural expression of this ability may differ to humans. A big challenge in the field of Comparative Psychology is the reliance on visible behaviours to make inferences about unseen cognition, and this should be kept in mind when concluding a cognitive ability is absent.

In some contexts, chimpanzees seem to be more socially motivated than the research discussed thus far may suggest. Chimpanzees can be trusting of a partner and demonstrate low-cost reciprocity (Engelmann et al, 2015) and in some cases help another to obtain a goal even if they do not immediately gain anything for themselves (Greenberg et al, 2010). Possibly, when we see examples of chimpanzees choosing to work alone rather than with a partner, the presence of food is a key factor. Chimpanzees can be tolerant and co-feed with group-mates (Koomen & Herrmann, 2018; Nolte et al., 2023), and share food (Jaeggi & Van Schaik, 2011). However, this food sharing may serve specific purposes, such as reciprocating a previous exchange or strengthening a certain social bond, and decisions about whether to share may be multifaceted (Silk et al., 2013). This is supported by the finding that tolerance between pairs of apes is important in cooperative tasks (Melis et al., 2006b), although the idea that tolerance explains bonobos' increased cooperativeness compared to chimpanzees has recently been challenged (Nolte et al., 2023). Looking at different contexts and removing the possible confound of food could be fruitful. For example, MacLean and Hare (2013) found that captive chimpanzees and bonobos preferentially chose social over solo play in some contexts. When looking at different contexts, different inferences about chimpanzees' social motivations can be drawn, and caution should be taken when inferring that they are not socially motivated from only looking at games with food involved, as many experiments do.

A major drawback of the work presented on joint action here is that chimpanzees may use different strategies or mechanisms when collaborating with a human compared to with a conspecific. The studies presented here focus on interactions between chimpanzees and human experimenters, which may confound conclusions made about chimpanzee interaction more generally. In humans, social factors can modulate joint action planning, for example, action accommodation may be more likely between members of the same ingroup (Dötsch & Schubö, 2015). Chimpanzees may have different impressions about the action capabilities of humans compared to conspecifics, or find it harder to predict action plans and imitate action from models with a different morphology and action repertoire. However, although these experimental coordination tasks between humans and chimpanzees are perhaps more artificial than joint actions between chimpanzees, it is worth noting that the chimpanzees included in these datasets interact with human caretakers and experimenters on a daily basis. For zoo-housed apes it may be valid to draw conclusions about joint action from human-chimpanzee coordination pairs. That being said, MacLean & Hare (2013) found that bonobos and chimpanzees chose to interact with an object with a human (social) compared to interacting with the object alone (solo), a pattern which was found with both familiar and unfamiliar humans. This same preference was not found when the social option was to interact with a conspecific, in which case subjects preferred the solo option. Further, some great ape subjects have shown increased communication or solicitation of human partners than conspecific partners in coordination tasks (Melis &

Rossano, 2022). Captive apes' social relationships with humans may evoke different expectations or motivations to interact than their relationships with one another ape, or they may more readily express joint action mechanisms in some social contexts over others. More information about how these joint action indicators manifest in chimpanzee dyads would help to establish a clearer understanding of chimpanzee joint action cognition, and possibly, virtual environment work could aid with this.

Another limitation inherent in primate cognition research is small sample sizes. Small samples often lead to under-powered studies (ManyPrimates et al., 2019), which can in turn make it difficult to detect effects of experimental manipulations, especially in the case of small effect sizes. Although the sample sizes across the studies presented here are typical for zoo-based primate cognition work (McEwen et al., 2022), and relatively large for touchscreen research (which has a mean sample size of 6.09 across primates, and 4.53 for great apes), this does not resolve the issue. Making conclusions about primate cognition based only on a small sample of primates, housed at only one or two facilities, may lead to biases in the field and may ignore extraneous variables impacting the data. Indeed, although the housing location (group) was included to control for variation between groups in some of the studies presented, and not for testing hypotheses, it is perhaps of interest that some significant effects of group were found on certain dependent measures. Multi-site collaborations are necessary to overcome this issue, such as ManyPrimates et al. (2019), which organises single experimental protocols to be implemented across numerous sites housing primates to achieve large sample sizes across diverse taxa. Findings from a single study with a single sample of primates may not necessarily replicate with other groups, or generalise to wild populations.

Issues of generalisability may be especially prevalent for spatial cognition. Wild primates traverse large, complex spaces and must develop the spatial-cognitive abilities to cope with this. In comparison, captive apes may spend their lives in a select few enclosures with freely available food, and so their spatial cognition skills may not need to develop to the same advanced levels as their wild counterparts (Normand et al., 2009). This idea is supported by contrasting findings between populations of golden tamarins; captive-reared animals reintroduced to a reserve showed a reduced ability to find their way and often got lost compared to wild tamarins (Menzel & Beck, 2000). There may be specific aspects of cognition that are unique to captive or wild populations, and these important differences should not be taken for granted.

We may at times consider experiments in captivity to be controlled studies of cognition, especially when comparing them to field work. However, there could be more consideration of the variables not always controlled for such as group mate presence, current food availability in an adjacent room, and group behaviour (for example, if the rest of the group are fighting). There could be several factors acting as proximate effects on cognitive ability beyond what we consider in the immediate testing space. While strategies such as randomisation, running multiple trials, and spreading testing across multiple days can all go some way toward eliminating the effects of extraneous variables, studying the impacts of these factors may be important for gaining a full picture of primate cognition. Some of these contextual factors may emulate aspects of wild primate ecology that affect wild primate behaviour, such as hierarchy disputes and food availability, and we could consider taking advantage of extraneous variables in zoos.

6.2 Future Directions

6.2.1 Joint Action: Definitions

To return to the definitions outlined by Duguid and Melis (2020), I would like to suggest expanding and elaborating on some categories. The third category, "Actively coordinated collaboration" seems to cover a very broad range of cognitive complexity. Figure 1 showed, when attempting to align it with other hierarchical explanations of joint action, there are several levels included in this third category. It may be helpful, in that case, to further breakdown this category.

I will outline below the different levels that could be included in 'actively coordinated collaboration' (levels 1 and 2) and shared intentional collaboration (level 3). These explanations will be from the perspective of one agent (A) who is engaging in a task with another agent (B).

Level 1: action representation

Level 1A: unidirectional action representation

In this first level, agent A represents their own actions and goals, and something about the actions of agent B, such as their walking trajectory towards prey, or their movement of one end of a string (Figure 34). In level 1A, this is only unidirectional. Agent B only considers their own actions. In this level, agent B could be a social tool, that would fall under Völter et al.'s (2015) levels 1 and 2. Agent A could act as a 'puppet master' and physically manipulate agent B, or exploit agent B's actions (such as in Schweinfurth et al. (2018) in which the subject used the actions of juveniles to obtain juice). Agent A could also adjust their actions to those of agent B and use their predictions about agent B's actions to inform their own action plan (as in the tool passing experiment in Chapter 2). This level could include more automatic processes of action representation as well as intentional monitoring of agent B's actions. The experiments presented in Chapters 2 and 3 are examples of how this level of coordination can be studied: action accommodation and action reversal/learning.

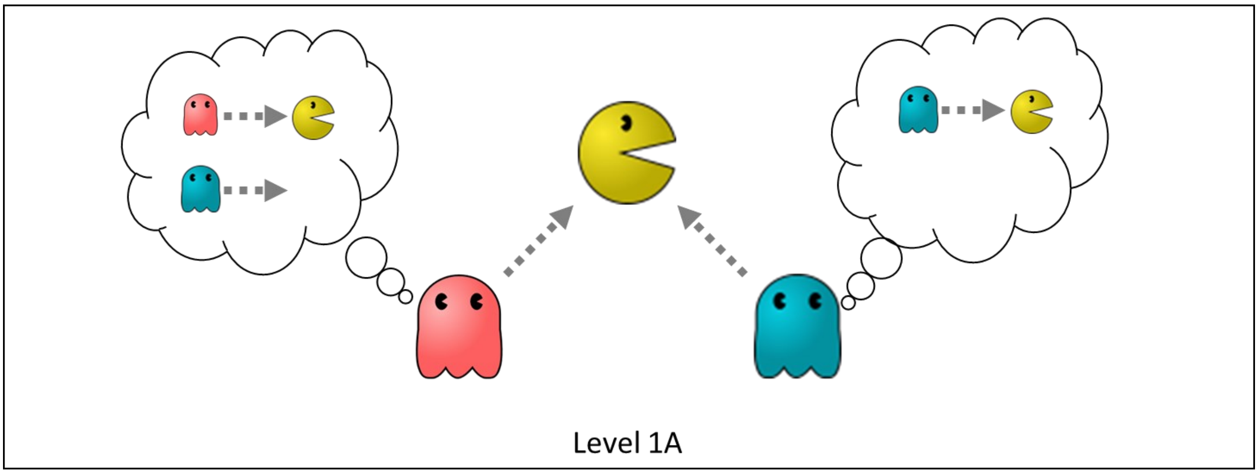

Figure 34: Level 1A (unidirectional action representation)

Level 1B: bidirectional action representation

Here, agent A is representing agent B's actions, and agent B is representing agent A's actions (Figure 35). They may adjust to one another's actions, or use their predictions about each other's actions to flexibly coordinate their actions.

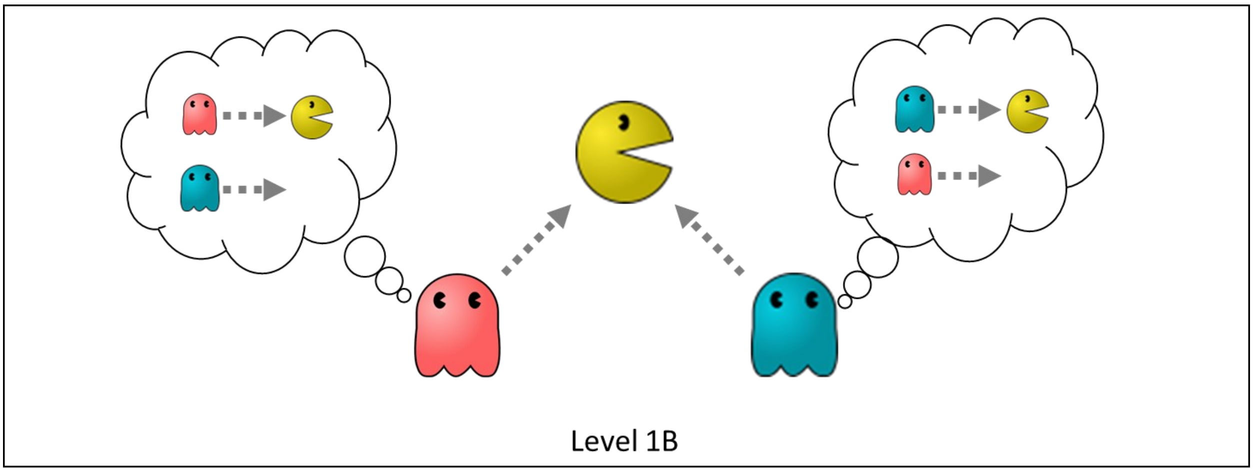

Figure 35: Level 1B (bidirectional action representation).

Level 2: mental state representation

Level 2A: unidirectional mental state representation

In this second level, agent A represents their own actions and goals, as well as the action and goal (or other mental state) of agent B (Figure 36). Parallels can be drawn between this level and Siposova & Carpenter's (2019) 'monitoring' level of social attention, as whilst agent A may consider what agent B is attending to, there is not yet 'common knowledge' between the agents, and agent B is still focused only on their own goal. Here, agent A may still use agent B as a social tool. This type of social tool use is labelled by Völter et al. (2015) as 'cooperative' (and also what they call 'level 3'), whereas the previous levels were referred to as 'coercive'. Now, agent A has to consider the goals of agent B and rely on agent B having complementary goals to use them as a social tool. The tool passing experiment in Chapter 2 could be adapted to study this level of coordination, for example, the experimenter's motivations or knowledge states could be experimentally manipulated.

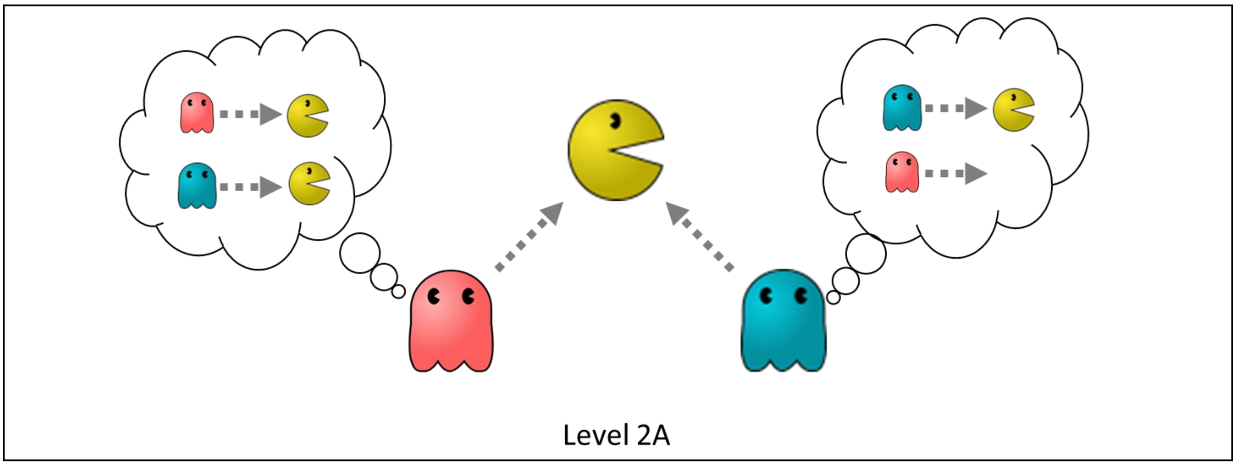

Figure 36: Level 2A (unidirectional mental state representation).

Level 2B: bidirectional mental state representation

Here, both agents A and B are representing each other's (as well as their own) goals/mental states (Figure 37). This is what Pacherie (2013) calls 'shared intentionality lite', as both agents are representing each other's goals – agent A represents their own goal and agent B's goal and sees that they are aligned. However, in this level, agents do not yet consider that each other both know this goal is aligned. In this level, joint social tool use could be observed. That is, both agents could use one another as tools to achieve their goals without conceiving of the goal as shared. This could be an interesting area of study, as it could lead to two agents attempting to manipulate one another, or working smoothly together. Almost all components of shared intentionality are present here, except the key aspect of conceiving of a goal as shared.

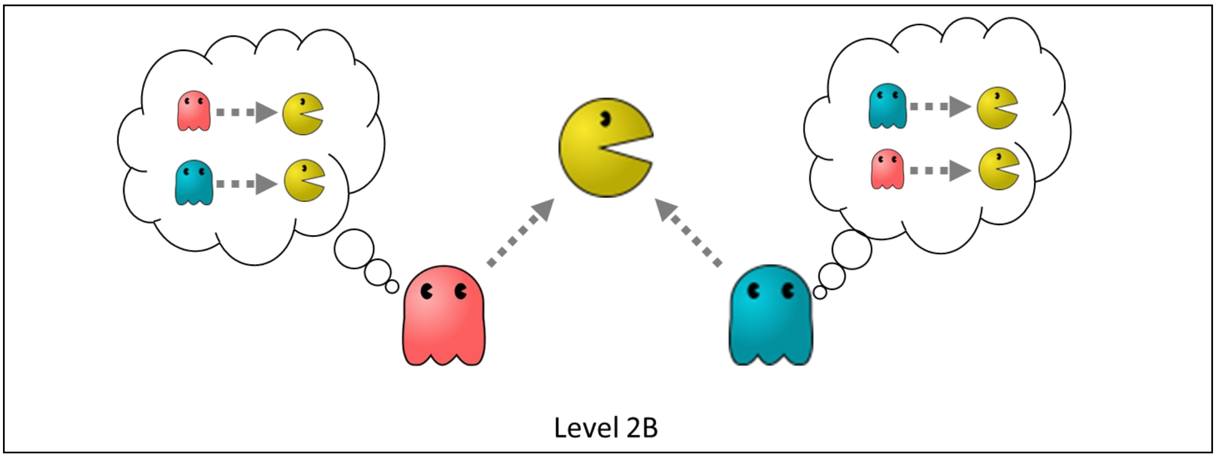

Figure 37: Level 2B (bidirectional mental state representation).

Level 3: recursive mental state representation

Finally, in shared intentionality, we see both agents representing their own actions and goals, and the fact that each other are representing those things, and some notion that the task is shared (Figure 38). This level could be compared to Siposova & Carpenter's (2019) 'mutual' and 'shared' attention, and is equivalent to Pacherie's (2013) 6th requirement for full shared intentionality.

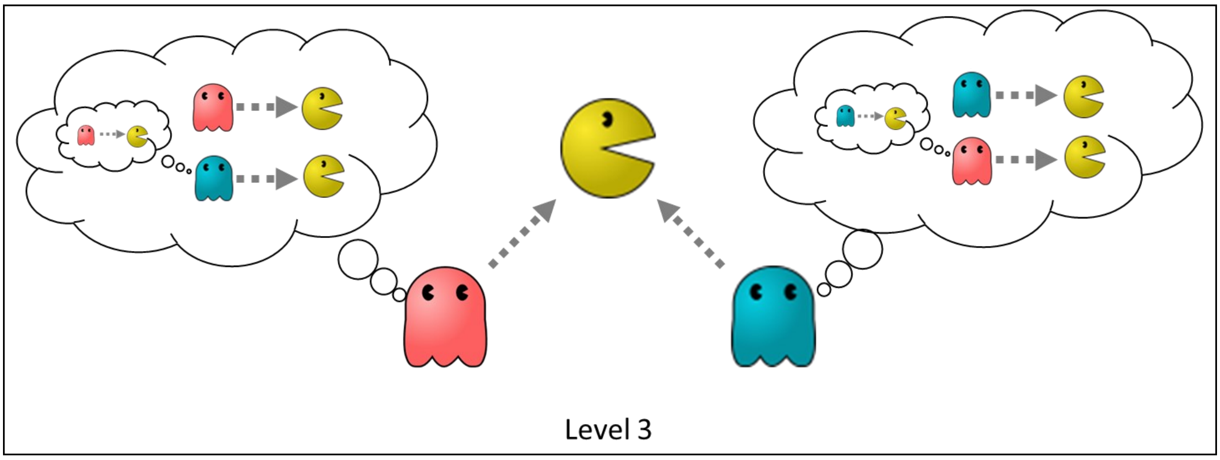

Figure 38: Level 3 (recursive mental state representation).

Action representation may remain consistent throughout these levels, or the level of specificity of that representation may vary. For example, if agent A does not have the knowledge or skillset required for agent B's actions, this representation may be vague (I know that agent B will do X, but I could not imagine all the components of X or exactly how X is executed). The specificity of the action representation may also decrease with increased trust in your partner. That is, if I do not know our goal is shared, I may pay more attention to your actions to ensure your part is done. Conversely, if I know that our goal is shared and I trust that you are committed to your role, I may pay less attention to your actions and instead focus on my own role. This is to say, the components of one level are not necessarily required for higher levels, and as the levels increase in complexity they may not do so cumulatively.

6.2.2 Joint action: Shared intentionality

Finding support for shared intentionality in chimpanzees has proven to be particularly challenging. Duguid and Melis (2020) suggest that evidence could come from communicating intention (as humans often do in shared tasks, for example, Duguid et al., 2014), but communication rates appear to be low between chimpanzee dyads in cooperative tasks (Bullinger et al., 2014b; Voinov et al., 2020). They also suggest that sharing the proceeds from a collaboration may indicate a consideration that the task was shared, and note that some field evidence suggests that chimpanzees may determine access to meat after a hunt proportionate to individual involvement (Boesch, 1994; Samuni et al., 2018). However, other factors may play a greater role, such as proximity and begging (Hamann et al., 2011; John et al., 2019; Gilby, 2006). Further, this idea relies on chimpanzees conceiving of fairness in reward distribution, which may not be the case, as a recent review found no evidence of inequity aversion across primates (Ritov et al., 2023) and ideas of ownership may not even be universal across human cultures (Rochat et al., 2014).

An alternative demonstration of shared intentionality could come from an information seeking paradigm. Great apes selectively seek information based on what they do not know, such as the location of food (Call & Carpenter, 2001), or the properties of a tool (Bohn et al., 2017). Apes also seek information more with increased stakes and increased time between baiting and retrieving (Call, 2010). So far, the evidence suggests that apes are flexible in their information search strategies, which could be harnessed to adapt an information-seeking paradigm to a social task, and ask whether apes also integrate another agent's knowledge into their decision to seek information.

Consider, for example, that you are driving a friend to their house after a party, and you have never been to their house. It may be that you do *not* look up information about the route, or the specific location of their house on the street, prior to the journey, as you know that your friend has that information. In this example, you use your knowledge of (1) your friend's knowledge state, and (2) your knowledge that you will act jointly. This could constitute a *common goal* (Siposova & Carpenter, 2019); you have aligned intentions with another. An additional consideration to elevate this to shared intentionally understanding is (3) your knowledge that your friend will share their knowledge with you. If all three considerations listed here are present, and one selectively seeks or does not seek information in response to the presence and absence of these factors, one might consider this to be evidence of shared intentionality that could conceivably be tested in apes.

It may be challenging to design a protocol in which apes can share knowledge with one another, but not infer this knowledge from subtle cues (such as excitement, arousal, or food grunts upon learning a food location). Moreover, it may be cognitively demanding to track multiple knowledge states as well as to plan for the future with those in mind. Before such a challenging task, it would be sensible to start a little simpler. First, one could test whether apes seek information pertaining to another agent's actions, such as what their partner can access (level 1). Secondly, one could test whether apes seek information about another's knowledge state, such as what their partner can see, or how they may perceive something (level 2). If apes seek information about what their partner can see and access, one could then test whether they modulate their own information seeking with their partner's knowledge state in mind. For example, if a subject's partner indicates a food location but did not see it baited, a subject may seek that information for themselves. Conversely, if the partner indicates a food location and they saw it baited, the subject may not seek that information for themselves as they trust the information based on their partner's knowledge state. This could, however, indicate social tool use, if they are able to use their partner's knowledge for their own goal. Only by adding an aspect of the task in which subjects' information seeking is also modulated by whether or not their partner will share the information, or whether they will engage in a shared task, can we perhaps begin seeing signs of shared intentionality.

6.2.3 Virtual Environments

The use of virtual environment technology in primate cognition is still in its early stages. Despite some promising results from previous work and the work presented here, questions remain about how these environments are represented by great apes and further study and validation is necessary before generalisations can be made to real-life navigation. It is perhaps premature to conclude that virtual environments are viewed as three-dimensional spaces by chimpanzees. Analysing travel trajectories in virtual environments, borrowing methods from field ecology such as path linearity assessments (as in Allritz et al., 2022) and change-point analysis (Noser & Byrne, 2014), could aid in elucidating how routes are planned, and which cues are responded to.

Future studies should consider the richness of virtual environments. In beginning this research, coming from an Experimental Psychology viewpoint, it seemed obvious that a ‘clean’ design should be implemented and the only cues to be presented should be those of interest. My views on this have changed over the course of my research, and considering how animals and humans find their way in the real world, a multitude of cues are present, and a richer, denser, and altogether more interesting environment may be needed to tap into navigation strategies in virtual worlds. A ‘messier’ environment would provide more cues to keep track of one’s location, as well as more visual proprioceptive information to aid optic flow as more objects in the world change size together as an avatar moves.

An interesting avenue for future work would be to directly compare movement through a virtual environment to movement in a real-life environment, such as simulating a virtual forest and comparing captive and wild apes. Another option could be recreating a virtual version of a familiar part of captive apes’ environment and assessing their understanding of equivalence between the two. There is abundant room for further progress with this technology, and virtual environment research could be implemented across species and across several topics.

6.3 Conclusion

The work presented here lends evidence to the hypothesis that chimpanzees engage in action representation during joint action, indicating Duguid and Melis' (2020) "actively coordinated collaboration". Chimpanzees are able to plan with another agent's actions in mind as well as possibly learn something about a partner's action through co-representation. Although more research is needed, the current evidence suggests that when chimpanzees are engaging in joint action, they do not only consider their own actions and roles, but also those of the agents they are collaborating with. It is yet to be determined what else they may represent about other agents during joint action, and what level of social tool use they may be capable of. Future work could focus on whether chimpanzees also represent other's mental states during cooperative tasks, whether this can be recursive, and whether or not shared intentionality is unique to humans or also an ability shared with other great apes.

The work in this thesis also shows that chimpanzees may not always choose the least effortful solution to a task. Whether this is an intentional indifference after weighing up options, or an issue of planning ability, remains unanswered here. The question of whether effort and efficiency are considered when chimpanzees choose to work alone also remains unanswered, but paradigms aiming to test this should always include a baseline assessment of solo effort preferences to confirm that chimpanzees have a clear preference for one apparatus or solution over another. Side preferences can be difficult for chimpanzees to overcome, and even when one option is harder, or even impossible, chimpanzees can be creatures of habit. Going forward, I have learned to carefully consider planning demands and physical cognition constraints when designing apparatuses for non-human primates and to not assume their preferences.

Finally, this thesis shows one of the earliest attempts to utilise virtual environment technology in primate cognition. It is very promising that apes were able to move a virtual avatar to find virtual food, even when this food fell out of sight behind a hedge. Furthermore, it is encouraging that at least some subjects were able to use a landmark to aid their foraging, and interesting to see that many could not when their training only consisted of learning from one angle. It is possible that with a different training regime or a translocation of a different nature, that more chimpanzees could learn to use virtual landmarks. In future endeavours, I will consider training that uses more salient cues, and which does not rely on the same repeated action response.

During social co-ordination, taking the perspective of a partner can be beneficial in order to understand their actions, viewpoint, or motivations. That is, there is a spatial aspect to joint action and the way in which a coordination space is represented could be important to understand for co-representation. Virtual environments could be further utilised to study aspects of social cognition, spatial cognition, and overlaps in the two.

References

Acredolo, L. P. (1978). Development of spatial orientation in infancy. *Developmental Psychology*, *14*(3), 224–234. https://doi.org/10.1037//0012-1649.14.3.224

Albiach-Serrano, A., Call, J., & Barth, J. (2010). Great apes track hidden objects after changes in the objects' position and in subject's orientation. *American Journal of Primatology*, *72*(4), 349–359. https://doi.org/10.1002/ajp.20790

Allen, J. A. (2019). Community through Culture: From Insects to Whales. *BioEssays*, *41*(11), 1900060. https://doi.org/10.1002/bies.201900060

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

Aquino, A., Paolini, D., Pagliaro, S., Migliorati, D., Wolff, A., Alparone, F. R., & Costantini, M. (2015). Group membership and social status modulate joint actions. *Experimental Brain Research*, *233*(8), 2461–2466. https://doi.org/10.1007/s00221-015-4316-7

Averly, B., Sridhar, V. H., Demartsev, V., Gall, G., Manser, M., & Strandburg-Peshkin, A. (2022). Disentangling influence over group speed and direction reveals multiple patterns of influence in moving meerkat groups. *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-17259-z

Baillargeon, R., Spelke, E. S., & Wasserman, S. (1985). Object permanence in five-month-old infants. *Cognition*, *20*(3), 191–208. https://doi.org/10.1016/0010-0277(85)90008-3

Ban, S. D., Boesch, C., N'guessan, A., Kouakou N'goran, E., Tako, A., & Janmaat, K. R. L. (2016). *Taï chimpanzees change their travel direction for rare feeding trees providing fatty fruits*. https://doi.org/10.1016/j.anbehav.2016.05.014

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

Bartus, R. T., Dean, R. L., III, & Fleming, D. L. (1979). Aging in the Rhesus Monkey: Effects on Visual Discrimination Learning and Reversal Learning1. *Journal of Gerontology*, *34*(2), 209–219. https://doi.org/10.1093/geronj/34.2.209

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). *Lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–8*.

Becchio, C., Sartori, L., Bulgheroni, M., & Castiello, U. (2008). The case of Dr. Jekyll and Mr. Hyde: A kinematic study on social intention. *Consciousness and Cognition*, *17*(3), 557–564. https://doi.org/10.1016/j.concog.2007.03.003

Bekkering, H., Abrams, R. A., & Pratt, J. (1995). Transfer of saccadic adaptation to the manual motor system. *Human Movement Science*, *14*(2), 155–164. https://doi.org/10.1016/0167-9457(95)00003-B

Beran, M. J., Beran, M. M., & Menzel, C. R. (2005a). Spatial Memory and Monitoring of Hidden Items Through Spatial Displacements by Chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *119*, 14–22. https://doi.org/10.1037/0735-7036.119.1.14

Beran, M. J., Beran, M. M., & Menzel, C. R. (2005b). Chimpanzees (Pan troglodytes) use markers to monitor the movement of a hidden item. *Primates*, *46*(4), 255–259. https://doi.org/10.1007/s10329-005-0150-z

Beran, M. J., & Minahan, M. F. (2000). Monitoring Spatial Transpositions by Bonobos (Pan paniscus) and Chimpanzees (P. troglodytes). *International Journal of Comparative Psychology*, *13*(1). https://doi.org/10.46867/C47W2D

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

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, *48*(3), 653–667. https://doi.org/10.1006/anbe.1994.1285

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, *78*(4), 547–573. https://doi.org/10.1002/ajpa.1330780410

Boesch, C., Boesch, P. C., & Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. Oxford University Press.

Boesch, C., & Tomasello, M. (1998). Chimpanzee and Human Cultures. *Current Anthropology*, *39*(5), 591–614. https://doi.org/10.1086/204785

Bohn, M., Allritz, M., Call, J., & Völter, C. J. (2017). Information seeking about tool properties in great apes. *Scientific Reports*, *7*(1), 10923. https://doi.org/10.1038/s41598-017-11400-z

Borke, H. (1975). Piaget's mountains revisited: Changes in the egocentric landscape. *Developmental Psychology*, *11*(2), 240. https://doi.org/10.1037/h0076459

Boukarras, S., Era, V., Aglioti, S. M., & Candidi, M. (2021). Competence-based social status and implicit preference modulate the ability to coordinate during a joint grasping task. *Scientific Reports*, *11*(1), 5321. https://doi.org/10.1038/s41598-021-84280-z

Bräuer, J., Call, J., & Tomasello, M. (2005). All Great Ape Species Follow Gaze to Distant Locations and Around Barriers. *Journal of Comparative Psychology*, *119*(2), 145. https://doi.org/10.1037/0735-7036.119.2.145

Brügger, R. K., Willems, E. P., & Burkart, J. M. (2023). Looking out for each other: Coordination and turn taking in common marmoset vigilance. *Animal Behaviour*, *196*, 183–199. https://doi.org/10.1016/j.anbehav.2022.11.007

Bullens, J., Iglói, K., Berthoz, A., Postma, A., & Rondi-Reig, L. (2010). Developmental time course of the acquisition of sequential egocentric and allocentric navigation strategies. *Journal of Experimental Child Psychology*, *107*(3), 337–350. https://doi.org/10.1016/j.jecp.2010.05.010

Bullinger, A. F., Melis, A. P., & Tomasello, M. (2011). Chimpanzees, Pan troglodytes, prefer individual over collaborative strategies towards goals. *Animal Behaviour*, *82*(5), 1135–1141. https://doi.org/10.1016/j.anbehav.2011.08.008

Bullinger, A. F., Melis, A. P., & Tomasello, M. (2014). Chimpanzees (Pan troglodytes) instrumentally help but do not communicate in a mutualistic cooperative task. *Journal of Comparative Psychology*, *128*(3), 251–260. https://doi.org/10.1037/a0035645

Bullinger, A. F., Wyman, E., Melis, A. P., & Tomasello, M. (2011). Coordination of Chimpanzees (Pan troglodytes) in a Stag Hunt Game. *International Journal of Primatology*, *32*(6), 1296–1310. https://doi.org/10.1007/s10764-011-9546-3

Burkart, J. M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., Huber, J., Isler, K., Kosonen, Z. K., Martins, E., Meulman, E. J., Richiger, R., Rueth, K., Spillmann, B., Wiesendanger, S., & van Schaik, C. P. (2014). The evolutionary origin of human hyper-cooperation. *Nature Communications*, *5*(1), 4747. https://doi.org/10.1038/ncomms5747

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science*, *10*(4), F31–F38. https://doi.org/10.1111/j.1467-7687.2007.00630.x

Butterfill, S. (2012). Joint Action and Development. *The Philosophical Quarterly*, *62*(246), 23–47. https://doi.org/10.1111/j.1467-9213.2011.00005.x

Byrne, R. W. (2002). Imitation of novel complex actions: What does the evidence from animals mean? In *Advances in the Study of Behavior* (Vol. 31, pp. 77–105). Academic Press. https://doi.org/10.1016/S0065-3454(02)80006-7

Call, J. (2003). Spatial rotations and transpositions in orangutans (Pongo pygmaeus) and chimpanzees (Pan troglodytes). *Primates*, *44*(4), 347–357. https://doi.org/10.1007/s10329-003-0048-6

Call, J. (2006). Descartes’ two errors: Reason and reflection in the great apes. In S. Hurley & M. Nudds (Eds.), *Rational Animals?* (pp. 219–234). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198528272.003.0010

Call, J. (2010). Do apes know that they could be wrong? *Animal Cognition*, *13*(5), 689–700. https://doi.org/10.1007/s10071-010-0317-x

Call, J., & Carpenter, M. (2001). Do apes and children know what they have seen? *Animal Cognition*, *3*(4), 207–220. https://doi.org/10.1007/s100710100078

Call, J., & Carpenter, M. (2002). *Three sources of information in social learning*. MIT Press.

Call, J., Hare, B., Carpenter, M., & Tomasello, M. (2004). “Unwilling” versus “unable”: Chimpanzees’ understanding of human intentional action. In *Developmental Science* (Vol. 7, pp. 488–498).

Call, J., & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans (Pongo pygmaeus). *Journal of Comparative Psychology*, *108*, 307–317. https://doi.org/10.1037/0735-7036.108.4.307

Cantwell, A., Buckholtz, J. W., Atencia, R., & Rosati, A. G. (2022). The origins of cognitive flexibility in chimpanzees. *Developmental Science*, e13266. https://doi.org/10.1111/DESC.13266

Carder, B., & Berkowitz, K. (1970). Rats’ Preference for Earned in Comparison with Free Food. *Science*, *167*(3922), 1273–1274. https://doi.org/10.1126/science.167.3922.1273

Chapman, K. M., Weiss, D. J., & Rosenbaum, D. A. (2010). Evolutionary Roots of Motor Planning: The End-State Comfort Effect in Lemurs. *Journal of Comparative Psychology*, *124*(2), 229–232. https://doi.org/10.1037/a0018025

Cheng, K. (1986). A purely geometric module in the rat’s spatial representation. *Cognition*, *23*(2), 149–178. https://doi.org/10.1016/0010-0277(86)90041-7

Cheng, K. (1989). The vector sum model of pigeon landmark use. *Journal of Experimental Psychology: Animal Behavior Processes*, *15*, 366–375. https://doi.org/10.1037/0097-7403.15.4.366

Cheng, K., & Jeffery, K. (2017). Spatial cognition. In *APA handbook of comparative psychology: Perception, learning, and cognition, Vol. 2* (pp. 463–483). American Psychological Association. https://doi.org/10.1037/0000012-021

Christie, L. A., Studzinski, C. M., Araujo, J. A., Leung, C. S. K., Ikeda-Douglas, C. J., Head, E., Cotman, C. W., & Milgram, N. W. (2005). A comparison of egocentric and allocentric age-dependent spatial learning in the beagle dog. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *29*(3), 361–369. https://doi.org/10.1016/j.pnpbp.2004.12.002

Clark, F. E., Gray, S. I., Bennett, P., Mason, L. J., & Burgess, K. V. (2019). High-Tech and Tactile: Cognitive Enrichment for Zoo-Housed Gorillas. *Frontiers in Psychology*, *10*. https://www.frontiersin.org/articles/10.3389/fpsyg.2019.01574

Clark, H. H. (2006). Social Actions, Social Commitments. In *Roots of Human Sociality*. Routledge.

Clay, A. W., Perdue, B. M., Gaalema, D. E., Dolins, F. L., & Bloomsmith, M. A. (2011). The use of technology to enhance zoological parks. *Zoo Biology*, *30*(5), 487–497. https://doi.org/10.1002/zoo.20353

Collett, M. (2010). How desert ants use a visual landmark for guidance along a habitual route. *Proceedings of the National Academy of Sciences*, *107*(25), 11638–11643. https://doi.org/10.1073/pnas.1001401107

Constable, M. D., Bayliss, A. P., Tipper, S. P., Spaniol, A. P., Pratt, J., & Welsh, T. N. (2016). Ownership Status Influences the Degree of Joint Facilitatory Behavior. *Psychological Science*, *27*(10), 1371–1378. https://doi.org/10.1177/0956797616661544

Constable, M. D., de Grosbois, J., Lung, T., Tremblay, L., Pratt, J., & Welsh, T. N. (2017). Eye movements may cause motor contagion effects. *Psychonomic Bulletin & Review*, *24*(3), 835–841. https://doi.org/10.3758/s13423-016-1177-4

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

Cox, M. V. (1975). The Other Observer in a Perspectives Task. *British Journal of Educational Psychology*, *45*(1), 83–85. https://doi.org/10.1111/j.2044-8279.1975.tb02301.x

Crawford, M. (1937). The cooperative solving of problems by young chimpanzees. *Comp Psychol Monogr*, *14*, 1–88.

Creem-Regehr, S. H., Gagnon, K. T., Geuss, M. N., & Stefanucci, J. K. (2013). Relating spatial perspective taking to the perception of other's affordances: Providing a foundation for predicting the future behavior of others. *Frontiers in Human Neuroscience*, *7*(SEP), 596. https://doi.org/10.3389/fnhum.2013.00596

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild Chimpanzees Inform Ignorant Group Members of Danger. *Current Biology*, *22*(2), 142–146. https://doi.org/10.1016/j.cub.2011.11.053

Curioni, A., Voinov, P., Allritz, M., Wolf, T., Call, J., & Knoblich, G. (2022). Human adults prefer to cooperate even when it is costly. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1973), 20220128. https://doi.org/10.1098/rspb.2022.0128

Dalmaso, M., Pavan, G., Castelli, L., & Galfano, G. (2011). Social status gates social attention in humans. *Biology Letters*, *8*(3), 450–452. https://doi.org/10.1098/rsbl.2011.0881

Davis, S. J., Schapiro, S. J., Lambeth, S. P., Wood, L. A., & Whiten, A. (2019). Behavioral conservatism is linked to complexity of behavior in chimpanzees (Pan troglodytes): Implications for cognition and cumulative culture. *Journal of Comparative Psychology*, *133*(1), 20–35. https://doi.org/10.1037/com0000123

Davis, V. A., Holbrook, R. I., & de Perera, T. B. (2018). The influence of locomotory style on three-dimensional spatial learning. *Animal Behaviour*, *142*, 39–47. https://doi.org/10.1016/j.anbehav.2018.06.002

de Blois, S. T., Novak, M. A., & Bond, M. (1998). Object permanence in orangutans (Pongo pygmaeus) and squirrel monkeys (Saimiri sciureus). *Journal of Comparative Psychology*, *112*, 137–152. https://doi.org/10.1037/0735-7036.112.2.137

Dolins, F. L. (2009). Captive cotton-top tamarins' (Saguinus oedipus oedipus) use of landmarks to localize hidden food items. *American Journal of Primatology*, *71*(4), 316–323. https://doi.org/10.1002/ajp.20654

Dolins, F. L., Klimowicz, C., Kelley, J., & Menzel, C. R. (2014). Using Virtual Reality to Investigate Comparative Spatial Cognitive Abilities in Chimpanzees and Humans. *J. Primatol*, *76*, 496–513. https://doi.org/10.1002/ajp.22252

Dombeck, D. A., Harvey, C. D., Tian, L., Looger, L. L., & Tank, D. W. (2010). Functional imaging of hippocampal place cells at cellular resolution during virtual navigation. *Nature Neuroscience*, *13*(11), 1433–1440. https://doi.org/10.1038/nn.2648

Dombeck, D. A., & Reiser, M. B. (2012). Real neuroscience in virtual worlds. *Current Opinion in Neurobiology*, *22*(1), 3–10. https://doi.org/10.1016/j.conb.2011.10.015

Dötsch, D., & Schubö, A. (2015). Social categorization and cooperation in motor joint action: Evidence for a joint end-state comfort. *Experimental Brain Research*, *233*(8), 2323–2334. https://doi.org/10.1007/s00221-015-4301-1

Duguid, S., & Melis, A. P. (2020). *How animals collaborate: Underlying proximate mechanisms*. *September 2019*, 1–18. https://doi.org/10.1002/wcs.1529

Duguid, S., Wyman, E., Bullinger, A. F., Herfurth-Majstorovic, K., & Tomasello, M. (2014). Coordination strategies of chimpanzees and human children in a Stag Hunt game. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1796), 20141973. https://doi.org/10.1098/rspb.2014.1973

Durand, K., & Lécuyer, R. (2002). Object permanence observed in 4-month-old infants with a 2D display. *Infant Behavior and Development*, *25*(3), 269–278. https://doi.org/10.1016/S0163-6383(02)00098-X

Egelkamp, C. L., & Ross, S. R. (2019). A review of zoo-based cognitive research using touchscreen interfaces. *Zoo Biology*, *38*(2), 220–235. https://doi.org/10.1002/zoo.21458

emmeans package, Version 1.8.5. (2019). *Comparisons and contrasts in emmeans*. https://cran.r-project.org/web/packages/emmeans/vignettes/comparisons.html#logs

Fernandez-Baizan, C., Arias, J. L., & Mendez, M. (2019a). Spatial memory in young adults: Gender differences in egocentric and allocentric performance. *Behavioural Brain Research*, *359*, 694–700. https://doi.org/10.1016/j.bbr.2018.09.017

Fernandez-Baizan, C., Arias, J. L., & Mendez, M. (2019b). Spatial orientation assessment in preschool children: Egocentric and allocentric frameworks. *Applied Neuropsychology: Child*, 1–23. https://doi.org/10.1080/21622965.2019.1630278

Fernández-Castro, V., & Pacherie, E. (2022). Commitments and the sense of joint agency. *Mind & Language*, *n/a*(n/a). https://doi.org/10.1111/mila.12433

Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, *424*(6950), Article 6950. https://doi.org/10.1038/nature01861

Fletcher, G. E., Warneken, F., & Tomasello, M. (2012). Differences in cognitive processes underlying the collaborative activities of children and chimpanzees. *Cognitive Development*, *27*(2), 136–153. https://doi.org/10.1016/J.COGDEV.2012.02.003

Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do Humans Integrate Routes Into a Cognitive Map? Map- Versus Landmark-Based Navigation of Novel Shortcuts. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*, 195–215. https://doi.org/10.1037/0278-7393.31.2.195

Frey, S. H., & Povinelli, D. J. (2012). Comparative investigations of manual action representations: Evidence that chimpanzees represent the costs of potential future actions involving tools. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1585), 48–58. https://doi.org/10.1098/rstb.2011.0189

Friard, O., & Gamba, M. (2016). *BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations—Friard—2016—Methods in Ecology and Evolution—Wiley Online Library*. https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12584

Garber, P. A., & Paciulli, L. M. (1997). Experimental Field Study of Spatial Memory and Learning in Wild Capuchin Monkeys (Cebus capucinus). *Folia Primatologica*, *68*(3–5), 236–253. https://doi.org/10.1159/000157250

Gazes, R. P., Templer, V. L., Rodgers, K. C., Mickelberg, J. L., & Stoinski, T. S. (2022). Information seeking in western lowland gorillas (Gorilla gorilla gorilla). *Learning & Behavior 2022*, *1*, 1–14. https://doi.org/10.3758/S13420-022-00554-0

Gerson, S. A., Bekkering, H., & Hunnius, S. (2015). Short-term Motor Training, but Not Observational Training, Alters Neurocognitive Mechanisms of Action Processing in Infancy. *Journal of Cognitive Neuroscience*, *27*(6), 1207–1214. https://doi.org/10.1162/jocn_a_00774

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, *71*(4), 953–963. https://doi.org/10.1016/j.anbehav.2005.09.009

Gonzalez, D. A., Studenka, B. E., Glazebrook, C. M., & Lyons, J. L. (2011). Extending end-state comfort effect: Do we consider the beginning state comfort of another? *Acta Psychologica*, *136*(3), 347–353. https://doi.org/10.1016/j.actpsy.2010.12.009

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Eweb:64029. https://repository.library.georgetown.edu/handle/10822/811357

Gray, J. R., Pawlowski, V., & Willis, M. A. (2002). A method for recording behavior and multineuronal CNS activity from tethered insects flying in virtual space. *Journal of Neuroscience Methods*, *120*(2), 211–223. https://doi.org/10.1016/S0165-0270(02)00223-6

Green, S. J., Boruff, B. J., & Grueter, C. C. (2019). *Chimpanzees use advanced spatial cognition to plan least-cost routes*. https://doi.org/10.1101/793562

Greenberg, J. R., Hamann, K., Warneken, F., & Tomasello, M. (2010). Chimpanzee helping in collaborative and noncollaborative contexts. *Animal Behaviour*, *80*(5), 873–880. https://doi.org/10.1016/J.ANBEHAV.2010.08.008

Gruber, T., & Zuberbühler, K. (2013). Vocal Recruitment for Joint Travel in Wild Chimpanzees. *PLOS ONE*, *8*(9), e76073. https://doi.org/10.1371/journal.pone.0076073

Grueneisen, S., Duguid, S., Saur, H., & Tomasello, M. (2017). Children, chimpanzees, and bonobos adjust the visibility of their actions for cooperators and competitors. *Scientific Reports*, *7*(1), 1–10. https://doi.org/10.1038/s41598-017-08435-7

Grund, C., Badihi, G., Graham, K. E., Safryghin, A., & Hobaiter, C. (2023). GesturalOrigins: A bottom-up framework for establishing systematic gesture data across ape species. *Behavior Research Methods*. https://doi.org/10.3758/s13428-023-02082-9

Hamann, K., Warneken, F., Greenberg, J. R., & Tomasello, M. (2011). Collaboration encourages equal sharing in children but not in chimpanzees. *Nature*, *476*(7360), Article 7360. https://doi.org/10.1038/nature10278

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance Allows Bonobos to Outperform Chimpanzees on a Cooperative Task. *Current Biology*, *17*(7), 619–623. https://doi.org/10.1016/J.CUB.2007.02.040

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

Hauge, T. C., Katz, G. E., Davis, G. P., Huang, D.-W., Reggia, J. A., & Gentili, R. J. (2021). High-Level Motor Planning Assessment During Performance of Complex Action Sequences in Humans and a Humanoid Robot. *International Journal of Social Robotics*, *13*(5), 981–998. https://doi.org/10.1007/s12369-020-00685-2

Haun, D. B. M., Rapold, C. J., Call, J., Janzen, G., & Levinson, S. C. (2006). *Cognitive cladistics and cultural override in Hominid spatial cognition*. www.pnas.orgcgidoi10.1073pnas.0607999103

Heesen, R., Bangerter, A., Zuberbühler, K., Iglesias, K., Neumann, C., Pajot, A., Perrenoud, L., Guéry, J.-P., Rossano, F., & Genty, E. (2021). Assessing joint commitment as a process in great apes. *IScience*, *24*(8), 102872. https://doi.org/10.1016/j.isci.2021.102872

Heesen, R., Bangerter, A., Zuberbühler, K., Rossano, F., Iglesias, K., Guéry, J.-P., & Genty, E. (2020). Bonobos engage in joint commitment. *Science Advances*, *6*(51), eabd1306. https://doi.org/10.1126/sciadv.abd1306

Heyes, C. (2012). Simple minds: A qualified defence of associative learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1603), 2695–2703. https://doi.org/10.1098/rstb.2012.0217

Heyes, C. (2016). Homo imitans? Seven reasons why imitation couldn't possibly be associative. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1686), 20150069. https://doi.org/10.1098/rstb.2015.0069

Hirata, S., & Fuwa, K. (2007). Chimpanzees (Pan troglodytes) learn to act with other individuals in a cooperative task. *Primates*, *48*(1), 13–21. https://doi.org/10.1007/s10329-006-0022-1

Ho, M. K., Abel, D., Correa, C. G., Littman, M. L., Cohen, J. D., & Griffiths, T. L. (2022). People construct simplified mental representations to plan. *Nature*, *606*(7912), Article 7912. https://doi.org/10.1038/s41586-022-04743-9

Hoffman, M. L., & Beran, M. J. (2006). Chimpanzees (Pan troglodytes) remember the location of a hidden food item after altering their orientation to a spatial array. *Journal of Comparative Psychology*, *120*(4), 389–393. https://doi.org/10.1037/0735-7036.120.4.389

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

Howard, L. H., Wagner, K. E., Woodward, A. L., Ross, S. R., & Hopper, L. M. (2017). Social Models Enhance Apes' Memory for Novel Events. *Scientific Reports*, *7*(1), 40926. https://doi.org/10.1038/srep40926

Hribar, A., Haun, D., & Call, J. (2011). Great apes' strategies to map spatial relations. *Animal Cognition*, *14*(511–523). https://doi.org/10.1007/s10071-011-0385-6

Jaeggi, A. V., & Van Schaik, C. P. (2011). The evolution of food sharing in primates. *Behavioral Ecology and Sociobiology*, *65*(11), 2125–2140. https://doi.org/10.1007/s00265-011-1221-3

Jang, H., Boesch, C., Mundry, R., Kandza, V., & Janmaat, K. R. L. (2019). Sun, age and test location affect spatial orientation in human foragers in rainforests. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1907), 20190934. https://doi.org/10.1098/rspb.2019.0934

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

Jensen, G. D. (1963). Preference for bar pressing over "freeloading" as a function of number of rewarded presses. *Journal of Experimental Psychology*, *65*, 451–454. https://doi.org/10.1037/h0049174

John, M., Duguid, S., Tomasello, M., & Melis, A. P. (2019). How chimpanzees (Pan troglodytes) share the spoils with collaborators and bystanders. *PLOS ONE*, *14*(9), e0222795. https://doi.org/10.1371/journal.pone.0222795

Johnston, R., Jones, K., & Manley, D. (2017). Confounding and collinearity in regression analysis: A cautionary tale and an alternative procedure, illustrated by studies of British voting behaviour | SpringerLink. *Qual Quant*, *52*, 1957–1976. https://doi.org/10.1007/s11135-017-0584-6

Juan, M.-C., Mendez-Lopez, M., Perez-Hernandez, E., & Albiol-Perez, S. (2014). Augmented Reality for the Assessment of Children's Spatial Memory in Real Settings. *PLOS ONE*, *9*(12), e113751. https://doi.org/10.1371/journal.pone.0113751

Kachel, U., & Tomasello, M. (2019). 3- and 5-year-old children's adherence to explicit and implicit joint commitments. *Developmental Psychology*, *55*(1), 80. https://doi.org/10.1037/dev0000632

Kano, F., & Call, J. (2014). Great Apes Generate Goal-Based Action Predictions: An Eye-Tracking Study. *Psychological Science*, *25*(9), 1691–1698. https://doi.org/10.1177/0956797614536402

Kano, F., & Call, J. (2017). Great Ape Social Attention. In S. Watanabe, M. A. Hofman, & T. Shimizu (Eds.), *Evolution of the Brain, Cognition, and Emotion in Vertebrates* (pp. 187–206). Springer Japan. https://doi.org/10.1007/978-4-431-56559-8_9

Király, I. (2009). The effect of the model's presence and of negative evidence on infants' selective imitation. *Journal of Experimental Child Psychology*, *102*(1), 14–25. https://doi.org/10.1016/j.jecp.2008.06.003

Kis, A., Huber, L., & Wilkinson, A. (2015). Social learning by imitation in a reptile (Pogona vitticeps). *Animal Cognition*, *18*(1), 325–331. https://doi.org/10.1007/s10071-014-0803-7

Kitchin, R. M. (1994). Cognitive maps: What are they and why study them? *Journal of Environmental Psychology*, *14*(1), 1–19. https://doi.org/10.1016/S0272-4944(05)80194-X

Knoblich, G., Butterfill, S., & Sebanz, N. (2011). Chapter three - Psychological Research on Joint Action: Theory and Data. In B. H. Ross (Ed.), *Psychology of Learning and Motivation* (Vol. 54, pp. 59–101). Academic Press. https://doi.org/10.1016/B978-0-12-385527-5.00003-6

Knoblich, G., & Sebanz, N. (2008). Evolving intentions for social interaction: From entrainment to joint action. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*((1499)), 2021–2031. https://doi.org/10.1098/rstb.2008.0006

Koomen, R., & Herrmann, E. (2018). The effects of social context and food abundance on chimpanzee feeding competition. *American Journal of Primatology*, *80*(2), e22734. https://doi.org/10.1002/ajp.22734

Koops, K., Soumah, A. G., van Leeuwen, K. L., Camara, H. D., & Matsuzawa, T. (2022). Field experiments find no evidence that chimpanzee nut cracking can be independently innovated. *Nature Human Behaviour*, *6*(4), Article 4. https://doi.org/10.1038/s41562-021-01272-9

Kourtis, D., Knoblich, G., Woźniak, M., & Sebanz, N. (2014). Attention Allocation and Task Representation during Joint Action Planning. *Journal of Cognitive Neuroscience*, *26*(10), 2275–2286. https://doi.org/10.1162/jocn_a_00634

Kozhevnikov, M., Motes, M. A., Rasch, B., & Blajenkova, O. (2006). Perspective-taking vs. Mental rotation transformations and how they predict spatial navigation performance. *Applied Cognitive Psychology*, *20*(3), 397–417. https://doi.org/10.1002/acp.1192

Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science*, *354*(6308), 110–114. https://doi.org/10.1126/science.aaf8110

Kuhlmeier, V. A., & Boysen, S. T. (2001). The effect of response contingencies on scale model task performance by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *115*, 300–306. https://doi.org/10.1037/0735-7036.115.3.300

Lai, Z. C., Moss, M. B., Killiany, R. J., Rosene, D. L., & Herndon, J. G. (1995). Executive system dysfunction in the aged monkey: Spatial and object reversal learning. *Neurobiology of Aging*, *16*(6), 947–954. https://doi.org/10.1016/0197-4580(95)02014-4

Leavens, D. A., Bard, K. A., & Hopkins, W. D. (2019). The mismeasure of ape social cognition. *Animal Cognition*, *22*(4), 487–504. https://doi.org/10.1007/s10071-017-1119-1

León, I., Cimadevilla, J. M., & Tascón, L. (2014). Developmental gender differences in children in a virtual spatial memory task. *Neuropsychology*, *28*(4), 485–495. https://doi.org/10.1037/neu0000054

Leopold, D. A., & Rhodes, G. (2010). A comparative view of face perception. *Journal of Comparative Psychology*, *124*(3), 233. https://doi.org/10.1037/a0019460

Levinson, S. C. (2003). *Space in Language and Cognition: Explorations in Cognitive Diversity*. Cambridge University Press.

Liebal, K., Call, J., Tomasello, M., & Pika, S. (2004). To move or not to move: How apes adjust to the attentional state of others. *Interaction Studies*, *5*(2), 199–219. https://doi.org/10.1075/is.5.2.03lie

Lingwood, J., Blades, M., Farran, E. K., Courbois, Y., & Matthews, D. (2015). The development of wayfinding abilities in children: Learning routes with and without landmarks. *Journal of Environmental Psychology*, *41*, 74–80. https://doi.org/10.1016/j.jenvp.2014.11.008

MacLean, E., & Hare, B. (2013). Spontaneous triadic engagement in bonobos (pan paniscus) and chimpanzees (pan troglodytes). *Journal of Comparative Psychology*, *127*(3), 245–255. https://doi.org/10.1037/a0030935

Manrique, H. M., & Call, J. (2015). Age-dependent cognitive inflexibility in great apes. *Animal Behaviour*, *102*, 1–6. https://doi.org/10.1016/j.anbehav.2015.01.002

ManyPrimates, Altschul, D. M., Beran, M. J., Bohn, M., Call, J., DeTroy, S., Duguid, S. J., Egelkamp, C. L., Fichtel, C., Fischer, J., Flessert, M., Hanus, D., Haun, D. B. M., Haux, L. M., Hernandez-Aguilar, R. A., Herrmann, E., Hopper, L. M., Joly, M., Kano, F., … Watzek, J. (2019). Establishing an infrastructure for collaboration in primate cognition research. *PLOS ONE*, *14*(10), e0223675. https://doi.org/10.1371/journal.pone.0223675

Marsh, H. L., Spetch, M. L., & Macdonald, S. E. (2011). Strategies in landmark use by orangutans and human children. *Animal Cognition*, *14*, 487–502. https://doi.org/10.1007/s10071-011-0382-9

McEllin, L., Knoblich, G., & Sebanz, N. (2018). Imitation from a joint action perspective. *Mind & Language*, *33*(4), 342–354. https://doi.org/10.1111/mila.12188

McEwen, E. S., Warren, E., Tenpas, S., Jones, B., Durdevic, K., Rapport Munro, E., & Call, J. (2022). Primate cognition in zoos: Reviewing the impact of zoo-based research over 15 years. *American Journal of Primatology*, *84*(10), e23369. https://doi.org/10.1002/ajp.23369

McGrew, W. C., & Rogers, M. E. (1983). Brief report: Chimpanzees, tools, and termites: New record from Gabon. *American Journal of Primatology*, *5*(2), 171–174. https://doi.org/10.1002/ajp.1350050207

Melis, A., Hare, B., & Tomasello, M. (2009). *Chimpanzees coordinate in a negotiation game*.

Melis, A. P., Hare, B., & Tomasello, M. (2006a). Chimpanzees recruit the best collaborators. *Science (New York, N.Y.)*, *311*(5765), 1297–1300. https://doi.org/10.1126/science.1123007

Melis, A. P., Hare, B., & Tomasello, M. (2006b). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Animal Behaviour*, *72*(2), 275–286. https://doi.org/10.1016/j.anbehav.2005.09.018

Melis, A. P., & Rossano, F. (2022). When and how do non-human great apes communicate to support cooperation? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1859), 20210109. https://doi.org/10.1098/rstb.2021.0109

Melis, A. P., & Tomasello, M. (2013). Chimpanzees' (Pan troglodytes) strategic helping in a collaborative task. *Biology Letters*, *9*(2), 20130009. https://doi.org/10.1098/rsbl.2013.0009

Melis, A. P., & Tomasello, M. (2019a). Chimpanzees (Pan troglodytes) coordinate by communicating in a collaborative problem-solving task. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1901), 20190408. https://doi.org/10.1098/rspb.2019.0408

Melis, A. P., & Tomasello, M. (2019b). Chimpanzees (*Pan troglodytes*) coordinate by communicating in a collaborative problem-solving task. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1901), 20190408. https://doi.org/10.1098/rspb.2019.0408

Menzel, C. R., & Beck, B. B. (2000). Homing and detour behavior in golden lion tamarin social groups. In *On the move: How and why animals travel in groups.* (pp. 299–326). University of Chicago Press.

Menzel, E. W. (1991). Chimpanzees (Pan troglodytes): Problem seeking versus the bird-in-hand, least-effort strategy. *Primates*, *32*(4), 497–508. https://doi.org/10.1007/BF02381940

Meulman, E. J. M., & van Schaik, C. P. (2013). Orangutan tool use and the evolution of technology. In C. M. Sanz, J. Call, & C. Boesch (Eds.), *Tool Use in Animals* (1st ed., pp. 176–202). Cambridge University Press. https://doi.org/10.1017/CBO9780511894800.012

Meyer, M., van der Wel, R. P. R. D., & Hunnius, S. (2013). Higher-order action planning for individual and joint object manipulations. *Experimental Brain Research*, *225*(4), 579–588. https://doi.org/10.1007/s00221-012-3398-8

Meyer, M., van der Wel, R. P. R. D., & Hunnius, S. (2016). Planning my actions to accommodate yours: Joint action development during early childhood. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1693), 329–332. https://doi.org/10.1098/rstb.2015.0371

Miall, R. C., & Wolpert, D. M. (1996). Forward Models for Physiological Motor Control. *Neural Networks*, *9*(8), 1265–1279. https://doi.org/10.1016/S0893-6080(96)00035-4

Michael, J., McEllin, L., & Felber, A. (2020). Prosocial effects of coordination – What, how and why? *Acta Psychologica*, *207*, 103083. https://doi.org/10.1016/j.actpsy.2020.103083

Michael, J., Sebanz, N., & Knoblich, G. (2016). The Sense of Commitment: A Minimal Approach. *Frontiers in Psychology*, *6*. https://www.frontiersin.org/articles/10.3389/fpsyg.2015.01968

Milward, S. J., & Carpenter, M. (2018). Joint action and joint attention: Drawing parallels between the literatures. *Social and Personality Psychology Compass*, *12*(4), e12377. https://doi.org/10.1111/spc3.12377

Miss, F. M., Adriaense, J. E. C., & Burkart, J. M. (2022). Towards Integrating Joint Action Research: Developmental and Evolutionary Perspectives on Co-representation. *Neuroscience & Biobehavioral Reviews*, 104924. https://doi.org/10.1016/J.NEUBIOREV.2022.104924

Miss, F. M., & Burkart, J. M. (2018). Corepresentation During Joint Action in Marmoset Monkeys (*Callithrix jacchus*). *Psychological Science*, *29*(6), 984–995. https://doi.org/10.1177/0956797618772046

Miss, F. M., Meunier, H., & Burkart, J. M. (2022). Primate origins of corepresentation and cooperative flexibility: A comparative study with common marmosets (Callithrix jacchus), brown capuchins (Sapajus apella), and Tonkean macaques (Macaca tonkeana). *Journal of Comparative Psychology*. https://doi.org/10.1037/COM0000315

Miss, F. M., Sadoughi, B., Meunier, H., & Burkart, J. M. (2022). Individual differences in co-representation in three monkey species (Callithrix jacchus, Sapajus apella and Macaca tonkeana) in the joint Simon task: The role of social factors and inhibitory control. *Animal Cognition 2022 25:6*, *25*(6), 1399–1415. https://doi.org/10.1007/S10071-022-01622-8

Montello, D. R. (2005). Navigation. In A. Miyake & P. Shah (Eds.), *The Cambridge Handbook of Visuospatial Thinking* (pp. 257–294). Cambridge University Press. https://doi.org/10.1017/CBO9780511610448.008

Mulcahy, N. J., & Call, J. (2006). How great apes perform on a modified trap-tube task. *Anim Cogn*, *9*, 193–199. https://doi.org/10.1007/s10071-006-0019-6

Muller, M. N., & Mitani, J. C. (2005). Conflict and Cooperation in Wild Chimpanzees. In *Advances in the Study of Behavior* (Vol. 35, pp. 275–331). Academic Press. https://doi.org/10.1016/S0065-3454(05)35007-8

Nagell, K., Olguin, R. S., & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (Pan troglodytes) and human children (Homo sapiens). *Journal of Comparative Psychology*, *107*, 174–186. https://doi.org/10.1037/0735-7036.107.2.174

Naik, H., Bastien, R., Navab, N., & Couzin, I. D. (2020). Animals in Virtual Environments. *IEEE Transactions on Visualization and Computer Graphics*, *26*(5), 2073–2083. https://doi.org/10.1109/TVCG.2020.2973063

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052–19059. https://doi.org/10.1073/pnas.0800375105

Negen, J., Heywood-Everett, E., Roome, H. E., & Nardini, M. (2018). Development of allocentric spatial recall from new viewpoints in virtual reality. *Developmental Science*, *21*(1). https://doi.org/10.1111/desc.12496

Neuringer, A. J. (1969). Animals Respond for Food in the Presence of Free Food. *Science*, *166*(3903), 399–401. https://doi.org/10.1126/science.166.3903.399

Noë, R. (2006). Cooperation experiments: Coordination through communication versus acting apart together. *Animal Behaviour*, *71*(1), 1–18. https://doi.org/10.1016/j.anbehav.2005.03.037

Nolte, S., & Call, J. (2021). *Targeted helping and cooperation in zoo-living chimpanzees and bonobos*. https://doi.org/10.1098/rsos.201688

Nolte, S., Sterck, E. H. M., & van Leeuwen, E. J. C. (2023). Does tolerance allow bonobos to outperform chimpanzees on a cooperative task? A conceptual replication of Hare et al., 2007. *Royal Society Open Science*, *10*(1), 220194. https://doi.org/10.1098/rsos.220194

Normand, E., Ban, S. D., & Boesch, C. (2009). Forest chimpanzees (Pan troglodytes verus) remember the location of numerous fruit trees. *Animal Cognition*, *12*(6), 797–807. https://doi.org/10.1007/s10071-009-0239-7

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

Normand, E., Dagui, S., & Boesch, C. (2009). Forest chimpanzees (Pan troglodytes verus) remember the location of numerous fruit trees. *Anim Cogn*, *12*, 797–807. https://doi.org/10.1007/s10071-009-0239-7

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

Odling-Smee, L., & Braithwaite, V. A. (2003). The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback. *Animal Behaviour*, *65*(4), 701–707. https://doi.org/10.1006/anbe.2003.2082

Okamoto-Barth, S., & Call, J. (2008). Tracking and inferring spatial rotation by children and great apes. *Developmental Psychology*, *44*(5), 1396. https://doi.org/10.1037/a0012594

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map: Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*, 171–175. https://doi.org/10.1016/0006-8993(71)90358-1

Pacherie, E. (2011). Framing Joint Action. *Review of Philosophy and Psychology*, *2*(2), 173–192. https://doi.org/10.1007/s13164-011-0052-5

Pacherie, E. (2013). Intentional joint agency: Shared intention lite. *Synthese*, *190*(10), 1817–1839. https://doi.org/10.1007/s11229-013-0263-7

Padrell, M., Amici, F., Córdoba, M. P., & Llorente, M. (2022). Cognitive enrichment in a social setting: Assessing the use of a novel food maze in sanctuary-housed chimpanzees. *Primates*, *63*(5), 509–524. https://doi.org/10.1007/s10329-022-00996-0

Pearce, J. M. (2014). *Animal Learning and Cognition: An Introduction* (3rd ed.). Psychology Press. https://doi.org/10.4324/9781315782911

Pepperberg, I. M., Willner, M. R., & Gravitz, L. B. (1997). Development of Piagetian object permanence in grey parrot (Psittacus erithacus). *Journal of Comparative Psychology*, *111*, 63–75. https://doi.org/10.1037/0735-7036.111.1.63

Péter, A., Range, F., & Pongrácz, P. (2011). Dogs cannot be deceived by virtual reality! Object permanence tasks on the touch screen. *Journal of Veterinary Behavior*, *6*(1), 57–58. https://doi.org/10.1016/j.jveb.2010.09.060

Pezzulo, G. (2011). Shared Representations as Coordination Tools for Interaction. *Review of Philosophy and Psychology*, *2*(2), 303–333. https://doi.org/10.1007/s13164-011-0060-5

Piaget, J. (1954). The development of object concept. In M. Cook (Ed.), *The construction of reality in the child* (pp. 3–96). Basic Books. https://doi.org/10.1037/11168-001

Platt, M., Brannon, E., Briese, T., & French, J. (1996). Differences in feeding ecology predict differences in performance between golden lion tamarins (Leontopithecus rosalia) and

Wied's marmosets (Callithrix kuhli) on spatial and visual memory tasks. *Learning & Behavior*, *24*, 384–393. https://doi.org/10.3758/BF03199010

Pope, S. M., Fagot, J., Meguerditchian, A., Watzek, J., Lew-Levy, S., Autrey, M. M., & Hopkins, W. D. (2020). Optional-switch cognitive flexibility in primates: Chimpanzees' (Pan troglodytes) intermediate susceptibility to cognitive set. *Journal of Comparative Psychology*, *134*(1), 98–109. https://doi.org/10.1037/com0000194

Potì, P. (2000). Aspects of spatial cognition in capuchins (Cebus apella): Frames of reference and scale of space. *Animal Cognition*, *3*(2), 69–77. https://doi.org/10.1007/s100710000062

Presotto, A., & Izar, P. (2010). Spatial reference of black capuchin monkeys in Brazilian Atlantic Forest: Egocentric or allocentric? *Animal Behaviour*, *80*(1), 125–132. https://doi.org/10.1016/j.anbehav.2010.04.009

Pritchard, D. J., & Healy, S. D. (2017). Homing and navigation. In *APA handbook of comparative psychology: Perception, learning, and cognition, Vol. 2* (pp. 485–508). American Psychological Association. https://doi.org/10.1037/0000012-022

Pritchard, D. J., Scott, R. D., Healy, S. D., & Hurly, T. A. (2016). Wild rufous hummingbirds use local landmarks to return to rewarded locations. *Behavioural Processes*, *122*, 59–66. https://doi.org/10.1016/j.beproc.2015.11.004

Ray, M., de Grosbois, J., & Welsh, T. N. (2017). Index of difficulty and side of space are accommodated during the selection and planning of a joint action. *Human Movement Science*, *54*, 197–209. https://doi.org/10.1016/j.humov.2017.05.009

Ray, M., & Welsh, T. N. (2011). Response Selection During a Joint Action Task. *Journal of Motor Behavior*, *43*(4), 329–332. https://doi.org/10.1080/00222895.2011.592871

Rekers, Y., Haun, D. B. M., & Tomasello, M. (2011). Children, but Not Chimpanzees, Prefer to Collaborate. *Current Biology*, *21*(20), 1756–1758. https://doi.org/10.1016/j.cub.2011.08.066

Ro, T., Friggel, A., & Lavie, N. (2007). Attentional biases for faces and body parts. *Visual Cognition*, *15*(3), 322–348. https://doi.org/10.1080/13506280600590434

Rochat, P., Robbins, E., Passos-Ferreira, C., Donato Oliva, A., Dias, M. D. G., & Guo, L. (2014). Ownership reasoning in children across cultures. *Cognition*, *132*(3), 471–484. https://doi.org/10.1016/j.cognition.2014.04.014

Rosati, A. G., Rodriguez, K., & Hare, B. (2014). The ecology of spatial memory in four lemur species. *Animal Cognition*, *17*(4), 947–961. https://doi.org/10.1007/s10071-014-0727-2

Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2007). The Evolutionary Origins of Human Patience: Temporal Preferences in Chimpanzees, Bonobos, and Human Adults. *Current Biology*, *17*(19), 1663–1668. https://doi.org/10.1016/j.cub.2007.08.033

Rosenbaum, D. A., & Jorgensen, M. J. (1992). Planning macroscopic aspects of manual control. *Human Movement Science*, *11*(1), 61–69. https://doi.org/10.1016/0167-9457(92)90050-L

Ruddle, R. A., Payne, S. J., & Jones, D. M. (1997). Navigating buildings in “desk-top” virtual environments: Experimental investigations using extended navigational experience. *Journal of Experimental Psychology: Applied*, *3*, 143–159. https://doi.org/10.1037/1076-898X.3.2.143

Samuni, L., Preis, A., Deschner, T., Crockford, C., & Wittig, R. M. (2018). Reward of labor coordination and hunting success in wild chimpanzees. *Communications Biology*, *1*(1), Article 1. https://doi.org/10.1038/s42003-018-0142-3

Sánchez-Amaro, A., Duguid, S., Call, J., & Tomasello, M. (2016). Chimpanzees coordinate in a snowdrift game. *Animal Behaviour*, *116*, 61–74. https://doi.org/10.1016/j.anbehav.2016.03.030

Sasaki, T., Mann, R. P., Warren, K. N., Herbert, T., Wilson, T., & Biro, D. (2018). Personality and the collective: Bold homing pigeons occupy higher leadership ranks in flocks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170038. https://doi.org/10.1098/rstb.2017.0038

Schluessel, V., & Bleckmann, H. (2005). Spatial memory and orientation strategies in the elasmobranch Potamotrygon motoro. *Journal of Comparative Physiology A: Neuroethology,* *Sensory, Neural, and Behavioral Physiology*, *191*(8), 695–706. https://doi.org/10.1007/s00359-005-0625-9

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

Schmitz, L., Vesper, C., Sebanz, N., & Knoblich, G. (2017). Co-representation of others' task constraints in joint action. *Journal of Experimental Psychology: Human Perception and Performance*, *43*, 1480–1493. https://doi.org/10.1037/xhp0000403

Schweinfurth, M. K., Baldridge, D. B., Finnerty, K., Call, J., & Knoblich, G. K. (2022). Inter-individual coordination in walking chimpanzees. *Current Biology*. https://doi.org/10.1016/J.CUB.2022.09.059

Schweinfurth, M. K., DeTroy, S. E., van Leeuwen, E. J. C., Call, J., & Haun, D. B. M. (2018). Spontaneous social tool use in Chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *132*(4), 455–463. https://doi.org/10.1037/com0000127

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

Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: Bodies and minds moving together. *Trends in Cognitive Sciences*, *10*(2), 70–76. https://doi.org/10.1016/J.TICS.2005.12.009

Sebanz, N., & Knoblich, G. (2021). Progress in Joint-Action Research. *Current Directions in Psychological Science*, *30*(2), 138–143. https://doi.org/10.1177/0963721420984425

Sebanz, N., Knoblich, G., & Prinz, W. (2003). Representing others' actions: Just like one's own? *Cognition*, *88*(3), B11–B21. https://doi.org/10.1016/S0010-0277(03)00043-X

Seed, A. M., Call, J., Emery, N. J., & Clayton, N. S. (2009). *Chimpanzees Solve the Trap Problem When the Confound of Tool-Use is Removed*. https://doi.org/10.1037/a0012925

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. (2013). Chimpanzees share food for many reasons: The role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*, *85*(5), 941–947. https://doi.org/10.1016/j.anbehav.2013.02.014

Silk, J. B., & House, B. R. (2016). The evolution of altruistic social preferences in human groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1687), 20150097. https://doi.org/10.1098/rstb.2015.0097

Siposova, B., & Carpenter, M. (2019). A new look at joint attention and common knowledge. *Cognition*, *189*, 260–274. https://doi.org/10.1016/j.cognition.2019.03.019

Smith, G. E., Bastos, A. P. M., Chodorow, M., Taylor, A. H., & Pepperberg, I. M. (2022). Contrafreeloading in kea (Nestor notabilis) in comparison to Grey parrots (Psittacus erithacus). *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-21370-6

Smith, G. E., Greene, D., Hartsfield, L. A., & Pepperberg, I. M. (2021). Initial evidence for eliciting contrafreeloading in grey parrots (Psittacus erithacus) via the opportunity for playful foraging. *Journal of Comparative Psychology*, *135*, 516–533. https://doi.org/10.1037/com0000295

Smolla, M., Alem, S., Chittka, L., & Shultz, S. (2016). Copy-when-uncertain: Bumblebees rely on social information when rewards are highly variable. *Biology Letters*, *12*(6), 20160188. https://doi.org/10.1098/rsbl.2016.0188

Stokes, E., & Byrne, R. (2001). Cognitive capacities for behavioural flexibility in wild chimpanzees (Pan troglodytes): The effect of snare injury on complex manual food processing. *Animal Cognition*, *4*, 11–28. https://doi.org/10.1007/s100710100082

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*. *14*(10), 995. https://doi.org/10.1038/nmeth.4399

Strachan, J. W. A., & Török, G. (2020). Efficiency is prioritised over fairness when distributing joint actions. *Acta Psychologica*, *210*, 103158. https://doi.org/10.1016/j.actpsy.2020.103158

Suchak, M., Eppley, T. M., Campbell, M. W., & de Waal, F. B. M. (2014). Ape duos and trios: Spontaneous cooperation with free partner choice in chimpanzees. *PeerJ*, *2*, e417. https://doi.org/10.7717/peerj.417

Tecwyn, E. C., Thorpe, S. K. S., & Chappell, J. (2013). A novel test of planning ability: Great apes can plan step-by-step but not in advance of action. *Behavioural Processes*, *100*, 174–184. https://doi.org/10.1016/J.BEPROC.2013.09.016

Tello-Ramos, M. C., Branch, C. L., Kozlovsky, D. Y., Pitera, A. M., & Pravosudov, V. V. (2019). Spatial memory and cognitive flexibility trade-offs: To be or not to be flexible, that is the question. *Animal Behaviour*, *147*, 129–136. https://doi.org/10.1016/j.anbehav.2018.02.019

Tennie, C. (2023). Focusing on relevant data and correcting misconceptions reaffirms the ape ZLS: Comment on “Blind alleys and fruitful pathways in the comparative study of cultural cognition” by Andrew Whiten. *Physics of Life Reviews*, *44*, 94–98. https://doi.org/10.1016/j.plrev.2022.12.007

Tennie, C., Call, J., & Tomasello, M. (2006). Push or Pull: Imitation vs. Emulation in Great Apes and Human Children. *Ethology*, *112*(12), 1159–1169. https://doi.org/10.1111/j.1439-0310.2006.01269.x

Thorpe, W. H. (1956). *Learning and instinct in animals* (pp. viii, 493). Harvard University Press.

Tinbergen, N. (1963). On aims and methods of Ethology. *Zeitschrift Für Tierpsychologie*, *20*(4), 410–433. https://doi.org/10.1111/j.1439-0310.1963.tb01161.x

Tokuyama, N., & Furuichi, T. (2017). Leadership of old females in collective departures in wild bonobos (Pan paniscus) at Wamba. *Behavioral Ecology and Sociobiology*, *71*(3), 55. https://doi.org/10.1007/s00265-017-2277-5

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, *55*, 189–208. https://doi.org/10.1037/h0061626

Tomasello, M. (2014). *A Natural History of Human Thinking*. Harvard University Press.

Tomasello, M. (2018). *A Natural History of Human Thinking*. Harvard University Press.

Tomasello, M. (2022). The coordination of attention and action in great apes and humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1859), 20210093. https://doi.org/10.1098/rstb.2021.0093

Tomasello, M., Melis, A. P., Tennie, C., Wyman, E., & Herrmann, E. (2012). Two Key Steps in the Evolution of Human Cooperation: The Interdependence Hypothesis. *Current Anthropology*, *53*(6), 673–692. https://doi.org/10.1086/668207

Török, G., Pomiechowska, B., Csibra, G., & Sebanz, N. (2019). *Rationality in Join Action: Maximizing Coefficiency in Coordination*. https://doi.org/10.1177/0956797619842550

Török, G., Stanciu, O., Sebanz, N., & Csibra, G. (2021). Computing Joint Action Costs: Co-Actors Minimize the Aggregate Individual Costs in an Action Sequence. *Open Mind*, *5*, 100–112. https://doi.org/10.1162/opmi_a_00045

Tsoar, A., Nathan, R., Bartan, Y., Vyssotski, A., Dell'Omo, G., & Ulanovsky, N. (2011). Large-scale navigational map in a mammal. *Proceedings of the National Academy of Sciences*, *108*(37), E718–E724. https://doi.org/10.1073/pnas.1107365108

Tuomela, R. (2007). *The Philosophy of Sociality: The Shared Point of View*. Oxford University Press.

Tweheyo, M., & Lye, K. A. (2003). Phenology of figs in Budongo Forest Uganda and its importance for the chimpanzee diet. *African Journal of Ecology*, *41*(4), 306–316. https://doi.org/10.1111/j.1365-2028.2003.00475.x

van den Brink, D., & Janzen, G. (2013). Visual spatial cue use for guiding orientation in two-to-three-year-old children. *Frontiers in Psychology*, *4*(DEC), 904. https://doi.org/10.3389/fpsyg.2013.00904

Vaughter, R. M., Smotherman, W., & Ordy, J. M. (1972). Development of object permanence in the infant squirrel monkey. *Developmental Psychology*, *7*, 34–38. https://doi.org/10.1037/h0032693

Vesper, C., van der Wel, R. P. R. D., Knoblich, G., & Sebanz, N. (2013). Are you ready to jump? Predictive mechanisms in interpersonal coordination. *Journal of Experimental Psychology Human Perception and Performance*, *39*(1), 48–61. https://doi.org/10.1037/a0028066

Visalberghi, E., Fragaszy, D. M., & Savage-Rumbaugh, S. (1995). Performance in a tool-using task by common chimpanzees (Pan troglodytes), bonobos (Pan paniscus), an orangutan (Pongo pygmaeus), and capuchin monkeys (Cebus apella). *Journal of Comparative Psychology*, *109*, 52–60. https://doi.org/10.1037/0735-7036.109.1.52

Voinov, P. V., Call, J., Knoblich, G., Oshkina, M., & Allritz, M. (2020). Chimpanzee Coordination and Potential Communication in a Two-touchscreen Turn-taking Game. *Scientific Reports*, *10*(1), 1–13. https://doi.org/10.1038/s41598-020-60307-9

Völter, C. J., & Call, J. (2014). Younger apes and human children plan their moves in a maze task. *Cognition*, *130*(2), 186–203. https://doi.org/10.1016/j.cognition.2013.10.007

Völter, C. J., Rossano, F., & Call, J. (2015). From exploitation to cooperation: Social tool use in orang-utan mother-offspring dyads. *Animal Behaviour*, *100*, 126–134. https://doi.org/10.1016/j.anbehav.2014.11.025

Warburton, K. (1990). The use of local landmarks by foraging goldfish. *Animal Behaviour*, *40*(3), 500–505. https://doi.org/10.1016/S0003-3472(05)80530-5

Warneken, F., Chen, F., & Tomasello, M. (2006). Cooperative activities in young children and chimpanzees. *Child Development*, *77*(3), 640–663. https://doi.org/10.1111/j.1467-8624.2006.00895.x

Weiss, D. J., Wark, J. D., & Rosenbaum, D. A. (2007). Monkey See, Monkey Plan, Monkey Do: The End-State Comfort Effect in Cotton-Top Tamarins (Saguinus oedipus). *Psychological Science*, *18*(12), 1063–1068. https://doi.org/10.1111/j.1467-9280.2007.02026.x

Whiten, A. (1996). Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *110*(1), 3. https://doi.org/10.1037/0735-7036.110.1.3

Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *112*, 270–281. https://doi.org/10.1037/0735-7036.112.3.270

Whiten, A. (2022). Blind alleys and fruitful pathways in the comparative study of cultural cognition. *Physics of Life Reviews*, *43*, 211–238. https://doi.org/10.1016/j.plrev.2022.10.003

Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *110*(1), 3. https://doi.org/10.1037/0735-7036.110.1.3

Whitham, W., & Washburn, D. A. (2020). Strategy use in probabilistic categorization by rhesus macaques (Macaca mulatta) and capuchin monkeys (Cebus [Sapajus] apella). *Journal of Comparative Psychology*, *134*(4), 379–390. https://doi.org/10.1037/COM0000221

Williams, J. M., Oehlert, G. W., Carlis, J. V., & Pusey, A. E. (2004). Why do male chimpanzees defend a group range? *Animal Behaviour*, *68*(3), 523–532. https://doi.org/10.1016/j.anbehav.2003.09.015

Wise, K. L., Wise, L. A., & Zimmermann, R. R. (1974). Piagetian object permanence in the infant rhesus monkey. *Developmental Psychology*, *10*, 429–437. https://doi.org/10.1037/h0036405

Wolf, W., & Tomasello, M. (2019). Visually attending to a video together facilitates great ape social closeness. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1907), 20190488. https://doi.org/10.1098/rspb.2019.0488

Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An Internal Model for Sensorimotor Integration. *Science*, *269*(5232), 1880–1882. https://doi.org/10.1126/science.7569931

Wood, S., Moriarty, K. M., Gardner, B. T., & Gardner, R. A. (1980). Object permanence in child and chimpanzee. *Animal Learning & Behavior*, *8*(1), 3–9. https://doi.org/10.3758/BF03209723

Wrangham, R. W. (1986). 16. Ecology and Social Relationships in Two Species of Chimpanzee. In *16. Ecology and Social Relationships in Two Species of Chimpanzee* (pp. 352–378). Princeton University Press. https://doi.org/10.1515/9781400858149.352

Wrangham, R. W. (1999). Evolution of coalitionary killing. *American Journal of Physical Anthropology*, *110*(S29), 1–30. https://doi.org/10.1002/(SICI)1096-8644(1999)110:29+<1::AID-AJPA2>3.0.CO;2-E

Yamamoto, S., Humle, T., & Tanaka, M. (2012). *Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals*. https://doi.org/10.1073/pnas.1108517109

Yang, Y., Merrill, E. C., & Wang, Q. (2019). Children's response, landmark, and metric strategies in spatial navigation. *Journal of Experimental Child Psychology*, *181*, 75–101. https://doi.org/10.1016/j.jecp.2019.01.005

Yoder, R. M., Clark, B. J., & Taube, J. S. (2011). Origins of landmark encoding in the brain. *Trends in Neurosciences*, *34*(11), 561–571. https://doi.org/10.1016/j.tins.2011.08.004

Zajonc, R. B. (1965). SOCIAL FACILITATION. *Science (New York, N.Y.)*, *149*(3681), 269–274. https://doi.org/10.1126/science.149.3681.269

Zander, S. L., & Judge, P. G. (2015). Brown Capuchin Monkeys (Sapajus apella) Plan Their Movements on a Grasping Task. *Article in Journal of Comparative Psychology*. https://doi.org/10.1037/a0038850

Zucca, P., Milos, N., & Vallortigara, G. (2007). Piagetian object permanence and its development in Eurasian jays (Garrulus glandarius). *Animal Cognition*, *10*(2), 243–258. https://doi.org/10.1007/s10071-006-0063-2

Appendices

Appendix A: Chapter 3 deviations from protocol/testing interruptions

Subject	Condition	Disruption	Solution
Eva	Co-operation	6 month interruption between learning and test phases	10 refresher trials before test phase. Also received repeat of test phase, after first attempt could reach the apparatus with fingers from the front.
Lucy	Co-operation	test phase interrupted	10 refresher learning trials before restarting test phase
Frek	Co-operation	6 month interruption partway through pre-test 2	Continued pre-test 2 until pass criterion reached
Frek	Co-operation	4 month interruption after 33 learning trials	Continued and completed remaining 67 learning trials before test phase
Qafzeh	Co-operation	6 month interruption after 32 learning trials	Continued and completed 68 learning trials learning trials before test phase
Qafzeh	Co-operation	4 month interruption after completing 97 learning trials	10 learning (3 to complete, 7 refresher) trials before beginning test phase
David	Object	6 month interruption after 26 learning trials	Continued and completed 47 learning trials learning trials
David	Object	4 month interruption after completing 73 learning trials	Continued and completed remaining 27 learning trials before test phase
Liberius	Object	6 month interruption after 45 learning trials	Continued and completed remaining 55 learning trials before test phase
Liberius	Object	4 month interruption partway through test phase	10 refresher learning trials before restarting test phase
Liberius	Object	3 month disruption partway through test phase	10 refresher learning trials before restarting test phase
Louis	Object	6 month interruption after 67 learning trials	Continued and completed remaining 33 learning trials before test phase
Kilimi	Object	6 month interruption after 70 learning trials	Continued and completed remaining 30 learning trials before test phase
Edith	Object	6 month interruption after 45 learning trials	Continued and completed remaining 55 learning trials before test phase
Edith	Object	4 month interruption after starting test phase	10 refresher learning trials before restarting test phase

Appendix B: Chapter 5 additional information

Fruit scatter randomisation in exploration stages: Four random distributions of fruit were created, and each was presented twice per session (with a session consisting of 8 trials). The order of these fruit distributions and order of starting positions (North-West, North, North-East, East, South-East, South, South-West, or West of the arena) were randomised for each counterbalance group, and changed for each experiment.

Table B1: Details of counterbalancing for Chapter 5. Subjects in grey were removed from the study after counterbalancing had been assigned.

Group	Subject	Counterbalance ID	Order	Experiment environment	Control environment	Food location
EDI	Frek	A	E - C	Field	Beach	West
LPZ	Frederike	B	E - C	Field	Beach	East
EDI	Qafzeh	C	E - C	Beach	Field	West
EDI	Eva	D	E - C	Beach	Field	East
EDI	Alex	E	C - E	Field	Beach	West
EDI	Velu	F	C - E	Field	Beach	East
EDI	Louie	G	C - E	Beach	Field	West
EDI	Kilimi	H	C - E	Beach	Field	East
LPZ	Azibo	A	E - C	Field	Beach	West
LPZ	Daza	B	E - C	Field	Beach	East
LPZ	Dorien	C	E - C	Beach	Field	West
LPZ	Robert	D	E - C	Beach	Field	East
LPZ	Lib	E	C - E	Field	Beach	West
LPZ	Riet	F	C - E	Field	Beach	East
LPZ	Tai	G	C - E	Beach	Field	West
LPZ	Fraukje	H	C - E	Beach	Field	East

Table B2: Details of side preferences for each subject in Chapter 5. 'Match' indicated whether or not their preferred side was the same as their training/experiment side.

Subject	Side pref assess	Side preference	Experiment side	Match?
Alex	Previous experiment	Right (78%, 134 trials)	Left	N
Frederike	Previous experiment	Right (97%, 70 trials)	Right	Y
Fraukje	Previous experiment	Left (68%, 80 trials)	Right	N

Dorien	Previous experiment	Right/no pref (59%, 74 trials)	Left	N
Tai	Side pref test	Left (71%, 24 trials)	Left	Y
Robert	Side pref test	Right (88%, 24 trials)	Right	Y
Riet	Side pref test	No pref (50%, 24 trials)	Right	NA
Azibo	Side pref test	Left (92%, 24 trials)	Left	Y
Daza	Side pref test	Left (72%, 25 trials)	Right	N
Eva	Side pref test	Right (67%, 24 trials)	Right	Y
Frek	Side pref test	Right (66%, 24 trials)	Left	N
Louis	Side pref test	Left/no pref (58%, 24 trials)	Left	Y
Velu	Side pref test	Left (81%, 54 trials)	Right	N
Qafzeh	Side pref test	Right/no pref (54%, 24 trials)	Left	N
Kilimi	Side pref test	Left/no pref (58%, 24 trials)	Right	N
Liberius	Side pref test	Left (75%, 24 trials)	Left	Y

Right group average right preference = 52.75%, Left group average left preference = 60.01%

Removing Daza and Riet due to dropping out:
Right group average right preference = 57.33%, Left group average left preference = 60.01%

Details of landmarks and arenas in each experiment:

- *Arena 1:* Grey walls, green hedges, and a grassy terrain.

  Arena 2: Red brick walls, brown hedges, and a sandy terrain.

- *Experiment 1 (Experimental condition):* I used a tree with pink leaves as a proximal, coincident landmark inside the hedge which contained food.
- *Experiment 1 (Control condition):* No landmarks were present; the arena only consisted of the four walls and two hedges.

- *Experiment 2, arena 1:* A central statue stood directly in between both hedges, which resembled a puffin. From the South, the face of the statue could be seen, and from the North, the back of the statue could be seen
- *Experiment 2, arena 2:* A central statue stood directly in between both hedges, which resembled a squirrel. From the South, the face of the statue could be seen, and from the North, the back of the statue could be seen
- *Experiment 3, arena 1:* In the South of the arena there were 9 bogs with reeds, in the North there were 9 hay bales
- *Experiment 3, arena 2:* In the South of the arena there were 9 water fountains, in the North there were 9 clusters of fir trees
- *Experiment 3, control transfer test:* In the South of the arena there were 9 geysers, in the North there were 9 clusters of sunflowers.

Table B3: Number of sessions of location learning stages for each subject across each experiment. Asterisks indicate stages in which the pass criterion was not met. Grey rows indicate that the subject was removed from transfer test analyses for that experiment.

Subject	**Phase**	**Location learning (visible)**	**Location learning (scaffolded)**	**Location learning (hidden)**	**Excluded?**
Eva	E1	2	1	4	
Eva	C1	2	7	2	
Eva	E2	3	1	7	
Eva	C2	10*	9	2	
Frek	E1	2	2	1	
Frek	C1	6	1	4	
Frek	E2	1	2	3	
Frek	C2	2	5	2	
Frek	E3	1	2	1	
Frek	C3	1	2	2	
Qafzeh	E1	2	9	1	
Qafzeh	C1	1	1	2	
Kilimi	C1	2	1	10	
Kilimi	E1	2	1	1	
Velu	C1	7	8	1*	y (not promoted and not passed

					after 10 sessions)
Velu	E1	1	1	5	y
Velu	C2	2	4	2	
Velu	E2	1	1	2	
Velu	C3	2	1	1	
Velu	E3	1	1	7	
Louis	C1	4	8	5	
Louis	E1	2	1	5	
Louis	C2	2	2	1	y
Louis	E2	2	3	11*	y
Louis	C3	3	4	9	
Louis	E3	9	5	10	
Fraukje	C1	1	1	1	
Fraukje	E1	2	1	1	
Fraukje	C2	1	1	1	
Fraukje	E2	1	1	1	
Fraukje	C3	1	1	2	
Fraukje	E3	1	1	1	
Frederike	E1	1	1	1	
Frederike	C1	1	1	1	
Frederike	E2	1	3	1	
Frederike	C2	1	1	3	
Frederike	E3	1	1	5	
Frederike	C3	2	3	15*	y
Dorien	E1	1	6	1	
Dorien	C1	1	5	1	
Dorien	E2	1	1	2	
Dorien	C2	1	1	2	
Tai	C1	2	6	1	
Tai	E1	4	1	1	
Tai	C2	3	1	1	
Tai	E2	2	1	1	
Tai	C3	2	1	1	
Tai	E3	1	1	1	
Azibo	E1	10*	9	1	
Azibo	C1	2	1	10*	y
Azibo	E2	1	10*	9	
Azibo	C2	1	1	1	
Liberius	C1	2	10*	10*	y
Liberius	E1	2	NA	NA	y
Alex	C1	1	2	1	
Alex	E1	1	1	1	
Alex	C2	1	1	1	
Alex	E2	1	3	2	
Alex	C3	1	1	1	

Alex	E3	1	2	5	
Robert	E1	4	1	3	
Robert	C1	1	2	4	
Robert	E2	2	2	1	
Robert	C2	1	1	1	
Robert	E3	3	1	1	
Robert	C3	2	1	1	

Table B4: Number of days between exploration and transfer test sessions for each subject. Grey rows indicate subjects who were exclude from transfer test analyses for that experiment.

Subject	**Phase**	**Date of last Exploration trial**	**Date of first transfer trial**	**No. days between last exploration and first transfer session**	**Excluded**
Eva	E1	15/06/2021	22/06/2021	7	
Eva	E2	07/04/2022	08/04/2022	1	
Frek	E1	25/06/2021	03/07/2021	8	
Frek	E2	26/11/2021	27/11/2021	1	
Frek	E3	27/02/2022	11/03/2022	12	
Qafzeh	E1	21/01/2022	22/01/2022	1	
Kilimi	E1	01/12/2022	02/12/2022	1	
Velu	E2	23/01/2022	31/01/2022	8	
Velu	E3	25/05/2022	10/06/2022	16	
Louis	E1	08/12/2021	09/12/2021	1	
Louis	E3	22/11/2022	25/11/2022	3	
Fraukje	E1	21/10/2021	22/10/2021	1	
Fraukje	E2	05/11/2021	08/11/2021	3	
Fraukje	E3	04/03/2022	07/03/2022	3	
Frederike	E1	10/11/2021	17/11/2021	7	
Frederike	E2	09/12/2021	10/12/2021	1	
Frederike	E3	08/03/2022	14/03/2022	6	y
Dorien	E1	20/10/2021	21/10/2021	1	
Dorien	E2	08/11/2021	09/11/2021	1	
Tai	E1	28/02/2022	04/03/2022	4	
Tai	E2	01/06/2022	03/06/2022	2	
Tai	E3	22/06/2022	24/06/2022	2	
Azibo	E2	23/07/2022	25/07/2022	2	
Alex	E1	21/11/2021	24/11/2021	3	
Alex	E2	15/02/2022	21/02/2022	6	
Alex	E3	22/04/2022	29/04/2022	7	
Robert	E1	07/03/2022	08/03/2022	1	
Robert	E2	08/06/2022	10/06/2022	2	
Robert	E3	06/07/2022	15/07/2022	9	
Velu	E1	22/09/2021	07/10/2021	15	y
Azibo	E1	10/05/2022	20/05/2022	10	y
Louis	E2	31/03/2022	01/04/2022	1	y

Table B5: Deviations from protocol/testing interruptions. Grey rows indicate exclusion from analyses.

Experiment 1	
Subject	**disruption/protocol discrepancy**
Robert	testing break between C1 hid and transfer (22 days), so required to reach criterion again before competing transfer
Louis	6 week testing interruption part-way through C1 scaff stage, no adjustment to protocol made, started where he left off
Eva	6 week testing interference after 4 trials of E1 transfer, moved back to E1 scaff
Frek	6 week testing interference after completing E1 hid, moved back to E1 scaff
Tai	received a session of C1 hid before passing scaff, moved back to scaff
Azibo	received a session of E1 scaff before passing vis, moved back to vis
Louis	received an extra two sessions of C1 scaff
Eva	received an extra 4 trials of C1 vis
Dorien	received an extra 2 trials of C1 vis
Eva	received an extra 2 trials of E1 hid
Kilimi	received an extra 1 trial of C1 vis
Eva	received an extra 1 trial of E1 vis
Experiment 2	
Subject	**disruption/protocol discrepancy**
Frek	testing break between C2 hid and transfer (19 days), so required to reach criterion again before competing transfer
Qafzeh	received 6 trials of E2 Exploration between trials 18 and 19 of C1 transfer
Kilimi	received an extra two sessions of C2 vis
Eva	received an extra 2 trials of C2 vis
Eva	received an extra 1 trial of E2 Exploration (final trial repeated)
Velu	received an extra trial of C2 vis
Experiment 3	
Subject	**disruption/protocol discrepancy**
Frek	did not receive refresher exploration or refresher hid sessions before transfer test, but time between last exploration and transfer comparable to other subjects
Alex	testing break between E3 hid and transfer (24 days), so repeated refresher stages (exploration short and hid)
Velu	received an extra session of E3 vis
Robert	received an extra session of C3 vis
Tai	received an extra session of C3 vis
Louis	received an extra 1 trial of E3 exploration
Experiment 1 (excluded)	
Subject	**disruption/protocol discrepancy**
Velu	received an extra 10 sessions of C1 hid, not passed and so excluded from analyses

Appendix C: VIFs of all models

Table C1: VIF values from models in Chapter 2.

Chapter 2	
Pre-test 1	Hand orientation: 1.00
	Trial: 1.00
	Group: 1.00
Experiment 1	Hand location: 1.00
	Trial: 1.00
	Group: 1.00
Experiment 2	Occupied hand: 1.00
	Trial: 1.00
	Group: 1.00
Experiment 3A	Barrier side: 1.00
	Group: 1.00
Experiment 3B	Barrier side: 1.00
	Group: 1.00
Experiment 4A	Box side: 1.47
	Group: 1.47
Experiment 4B	Box side: 1.06
	Group: 1.06

Table C2: VIF values from models in Chapter 3.

Chapter 3	
Experiment 1A: Right/left choice	High effort box (left/right): Na
Experiment 2: Right/left choice	Blocked box (left/right): 1.01
	Blocked box (high/low): 1.01
Experiment 1B: Right/left choice	High effort box (left/right): NA

Table C3: VIF values from models in Chapter 4.

Chapter 4	
Flip frequency	Condition: 1.00
	Trial: 1.00
Flip frequency (subjects who flipped)	Condition: 1.01
	Trial: 1.01
Flip type	Condition: NA
Flip latency	Condition: 1.34
	Trial: 1.34
Pull frequency	Condition: 1.02

	Trial: 1.02
Pull latency	Condition: 1.04
	Trial: 1.04
Frequency of leaving	Condition: 1.00
	Trial: 1.00
Latency to leave	Condition: 1.07
	Trial: 1.07

Table C4: VIF values from models in Chapter 5.

Chapter 5	
Experiment 1: Location learning	Condition: 1.00
	Order: 1.00
	Group: 1.00
Experiment 1: transfer test	Condition: 1.01
	Block: 1.01
	Trial: 1.00
	Group: 1.00
Experiment 1: transfer test (experience)	Condition: 1.01
	Order: 1.01
	Trial: 1.00
	Group: 2.14
	Experience: 2.13
Experiment 2: transfer test	Condition: 1.05
	Order: 1.06
	Trial: 1.01
	Group: 1.01
Experiment 3: transfer test	Condition: 1.22
	Order: 1.22
	Trial: 1.00
	Group: 1.00

Appendix D: Ethical approval documents

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

4 February 2019

Dear Emma

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 24th January 2019. The following documents have been reviewed:

1. Animal Ethics Form

Project Title:	Do chimpanzees represent and facilitate the action of a coagent?		
Researcher's Name:	Emma McEwen		
Supervisor:	Professor Josep Call		
Approved on:	01/02/2019	**Approval Expiry:**	01/02/2024

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Professor Josep Call (Supervisor)
Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071
The University of St Andrews is a charity registered in Scotland: No SC013532

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

3 February 2020

Dear Emma

Thank you for submitting your application for amendment which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 29th January 2020. The following documents have been reviewed:

1. Application for change(s) to a School Ethics Committee Form
2. Amended Animal Ethics Form

Project Title:	Do non-human great apes represent and facilitate the action of a coagent?		
Researcher:	Emma McEwen		
Supervisor:	Professor Josep Call		
Original Approval:	01/02/2019	**Amendment Approval**:	03/02/2019
Approval Expiry:	01/02/2024		
SEC Approval Code:	166		

The School of Psychology & Neuroscience Ethics Committee approves the amendment to this study from an ethical point of view.

Approval is given for five years from the date of approval of the original application. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

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Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Prof Josep Call
School Ethics Committee
Dr Tamara Lawson (Home Office Liaison Officer)

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

4th September 2019

Dear Elizabeth and Emma

Thank you for submitting your application which was considered by the Psychology & Neuroscience School Ethics Committee on 20th August 2018. The following documents have been reviewed:

1. Animal Ethics Form
2. Apparatus Graphics and Procedure
   To follow:
   External Permission: Budongo Research Unit (BRU)

Project Title:	Communication and Coordination in a Two-Action Task		
Researchers' Names:	Elizabeth Warren, Emma McEwen, Dr Manon Schweinfurth		
Supervisor:	Professor Josep Call		
Approved on:	28/08/2019	**Approval Expiry:**	28/08/2024

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Professor Josep Call (Supervisor)
Dr Tamara Lawson (Home Office Liaison Officer)

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

4 December 2019

Dear Elizabeth and Emma

Thank you for submitting your application for amendment which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 28th November 2019. The following documents have been reviewed:

1. Application for change(s) to a School Ethics Committee Form
2. Amended Animal Ethics Form

Project Title:	Communication and Coordination in a Two-Action Task		
Researchers:	Elizabeth Warren, Emma McEwen and Dr Manon Schweinfurth		
Supervisor:	Professor Josep Call		
Original Approval:	28/08/2019	**Amendment Approval**:	03/12/2019
Approval Expiry:	28/08/2024		
SEC Approval Code:	181		

The School of Psychology & Neuroscience Ethics Committee approves the amendment to this study from an ethical point of view.

Approval is given for five years from the date of approval of the original application. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and a further application for amendment submitted where appropriate.

Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Professor Josep Call
Dr Tamara Lawson (Home Office Liaison Officer)

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

19th February 2021

Dear Louise and Emma

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 18th February 2021. The following documents have been reviewed:

1. Animal Ethics Form
   To follow:
   Budongo Research Unit (BRU) project approval
   Copy of Risk Assessment

Project Title:	Do chimpanzees consider action effort and efficiency when choosing to co-ordinate?		
Researchers:	Louise Mackie and Emma McEwen		
Supervisors:	Professor Josep Call and Dr Sophie Edwards		
Approved on:	18/02/2021	**Approval Expiry:**	18/02/2026
SEC Approval Code:	204		

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Professor Josep Call
Dr Sophie Edwards
Home Office Liaison Officer

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

27 June 2022

Dear Emma

Thank you for submitting your application for amendment which was considered by the Psychology & Neuroscience School Ethics Committee on the 27th June 2022. The following documents have been reviewed:

1. Application for change(s) to a School Ethics Committee Form
2. Amended Animal Ethics Form

Project Title:	Do chimpanzees consider action effort?		
Researchers:	Louise Mackie, Emma McEwen		
Supervisor/PI:	Professor Josep Call and Dr Sophie Edwards		
Original Approval:	18/02/2021	**Amendment Approval**:	27/06/2022
Approval Expiry:	18/02/2026		
Approval Code:	PS16373	**Former SEC Code**:	204

The School of Psychology & Neuroscience Ethics Committee approves the amendment to this study from an ethical point of view.

Approval is given for five years from the date of approval of the original application. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and a further application for amendment submitted where appropriate.

Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Dr Helen Sunderland
Administrator to the School Ethics Committee

Ccs Professor Josep Call
Dr Sophie Edwards

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

19 November 2018

Dear Emma and Matthias

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on 15th November 2018. The following documents have been reviewed:

1. Animal Ethics Form

Project Title:	Virtual Environment Tasks with Chimpanzees in Edinburgh Zoo using Touchscreens		
Researchers' Names:	Emma McEwen and Dr Matthias Allritz		
Supervisors:	Professor Josep Call		
Approved on:	15/11/2018	**Approval Expiry:**	15/11/2023

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Professor Josep Call (Supervisor)
Dr Tamara Lawson (Home Office Liaison Officer)

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

30 April 2019

Dear Emma

Thank you for submitting your application for amendment which was considered by the Psychology & Neuroscience School Ethics Committee on the 30th April 2019. The following documents have been reviewed:

1. Application for change(s) to a School Ethics Committee Form
2. Amended Animal Ethics Form

Project Title:	Virtual Environment Tasks with Chimpanzees using Touchscreens		
Researchers:	Emma McEwen and Dr Matthias Allritz		
Supervisor:	Professor Josep Call		
Original Approval:	15/11/2018	**Amendment Approval**:	30/04/2019
Approval Expiry:	15/11/2023		

The School of Psychology & Neuroscience Ethics Committee approves the amendment to this study from an ethical point of view.

Approval is given for five years from the date of approval of the original application. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and a further application for amendment submitted where appropriate.

Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Professor Josep Call (Supervisor)
Dr Tamara Lawson (Home Office Liaison Officer)

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

18 October 2019

Dear Emma

Thank you for submitting your application for amendment which was considered by the Psychology & Neuroscience School Ethics Committee meeting on 17 October 2019. The following documents have been reviewed:

1. Application for change(s) to a School Ethics Committee Form
2. Amended Animal Ethics Form

Project Title:	Virtual Environment Tasks with Chimpanzees and Orang-utans using Touchscreens		
Researchers:	Emma McEwen and Matthias Allritz		
Supervisor:	Professor Josep Call		
Original Approval:	15/11/2018	**Amendment Approval**:	18/10/2019
Approval Expiry:	15/11/2023		

The School of Psychology & Neuroscience Ethics Committee approves the amendment to this study from an ethical point of view.

Approval is given for five years from the date of approval of the original application. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and a further application for amendment submitted where appropriate.

Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Professor Josep Call (Supervisor)
School Ethics Committee
Dr Tamara Lawson (Home Office Liaison Officer)