# Chimpanzees demonstrate a behavioural signature of human joint action

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## ABSTRACT

The strength of human society can largely be attributed to the tendency to work together to achieve outcomes that are not possible alone. Effective social coordination benefits from mentally representing a partner's actions. Specifically, humans optimize social coordination by forming internal action models adapted to joint rather than individual task demands. To what extent do humans share the cognitive mechanisms that support optimal human coordination and collaboration with other species? An ecologically inspired joint handover-to-retrieve task was systematically manipulated across several experiments to assess whether joint action planning in chimpanzees reflects similar patterns to humans. Chimpanzees' chosen handover locations shifted towards the location of the experimenter's free or unobstructed hand, suggesting they represent the constraints of the joint task even though their individual half of the task was unobstructed. These findings indicate that chimpanzees and humans may share common cognitive mechanisms or predispositions that support joint action.

## 1. Introduction

The human ability to fluidly coordinate and adapt to a coordinative partner's needs is a cornerstone of everyday life. Yet, the ease with which coordination occurs and the relative infrequency of coordinative failures belies the complexity of the cognitive processes that may be deployed for a successful and efficient interaction. Indeed, the tendency to collaborate and coordinate can be considered a potential evolutionary advantage for the human species (Tomasello, 2014). The present paper asks whether the cognitive mechanisms and behavioural patterns that humans have evolved to achieve smooth and successful coordinative outcomes (Sebanz & Knoblich, 2021) are shared with close evolutionary ancestors. Specifically, do chimpanzees represent the required actions of both themselves and a human co-agent in a joint handover-to-retrieve task?

Humans act on the environment via motor commands. Internal forward models for action provide a representation of action possibilities and a means to predict the best potential path to achieve an end goal relative to the environment's demands (Wolpert, Ghahramani, &

Jordan, 1995). These forward models are continually updated and adjusted relative to experience, gradually refining internal action representations alongside their expected consequences. A further advantage of predictive models is that they allow for faster and more fluid motor adaptation. Rather than responding to the environment, one can proactively compensate for expected sensory feedback (Wolpert & Miall, 1996). Consider stepping onto a broken escalator. The body adjusts for the predicted sensory experience of movement, which ordinarily would ensure a stable gait as the body transfers from self-generated locomotion alone to combined externally and internally generated locomotion. However, when the associated sensory experience of movement does not occur, a slower adjustment based on actual sensory experience is required. Meaning, internal models provide the scaffolding for fast and fluid interactions with the world, that can be adjusted when the sensory experience does not match that which was predicted.

In a social environment, internal models for action may be accessed to understand and predict the actions of others (Flanagan & Johansson, 2003; Wolpert, Doya, & Kawato, 2003). These predictive models can be integrated within a representation shared by all co-agents that considers

the joint task as a whole (Pezzulo, 2011; Sebanz & Knoblich, 2021). This shared representation will often be observable via the selection of individual motor commands that maximise the efficiency of the joint goal rather than any individual component (Curioni, Vesper, Knoblich, & Sebanz, 2019; Török, Pomiechowska, Csibra, & Sebanz, 2019).

### 1.1. Joint action in non-human primates?

For the purposes of this paper, we define 'joint action' as any event whereby two or more agents coordinate spatially and temporally to alter the environment (Sebanz, Bekkering, & Knoblich, 2006). Whilst previous research has shown that chimpanzees are capable of working together in certain contexts [e.g. hunting, (Boesch & Boesch, 1989); pulling ropes attached to baited trays with a partner (Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2009)], the cognitive mechanisms used by chimpanzees in such situations remain a topic of debate. It is possible that separate individuals may only appear to be collaborating without intending to coordinate (Duguid & Melis, 2020). In such cases of potential 'by-product' collaboration, two agents could react to an external cue, like the presence of prey, and act independently but in a complementary manner with the individual aim of acquiring their goal. Coordinative behaviour could also be influenced by another agent's presence ('socially influenced collaboration') without understanding that the other agent has similar goals and intentions and without considering how the agent's roles and actions contribute to the coordinative outcome. Last, it may be possible that chimpanzees can engage in 'actively coordinated collaboration' whereby they have an understanding of the goals and intentions of the coordinative partner, and they consider how the partner's role and actions contribute to the coordinative outcome.

Speaking to action planning processes, non-human 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, Weiss, & Rosenbaum, 2010), chimpanzees (Frey & Povinelli, 2012), cotton-top tamarins (Weiss, Wark, & Rosenbaum, 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 illustrated above, shared representations are thought to be necessary for successful joint action in humans (Pezzulo, 2011). Common marmosets exhibit co-representation (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, Hare, & Tomasello, 2006). Also, chimpanzees alter the visibility of their actions differently to co-operators and competitors, indicating perspective-taking (Grueneisen, Duguid, Saur, & Tomasello, 2017). Similarly, chimpanzees and bonobos position themselves within an experimenter's field of view to visually gesture for food (Liebal, Call, Tomasello, & Pika, 2004). Thus, it is plausible that chimpanzees also possess cognitive processes that support joint action beyond minimal forms of non-intentional "emergent coordination" (Knoblich, Butterfill, & Sebanz, 2011).

### 1.2. The present study

If chimpanzees can flexibly adapt their actions in response to joint task constraints, 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 understanding and planning in chimpanzees. A joint handover-to-retrieve task reflecting an ecological approach to studying joint action in both humans and chimpanzees, was developed. In human handover tasks, participants typically orient objects so a co-agent may more comfortably

grasp or interact with that object (Constable et al., 2016; Gonzalez, Studenka, Glazebrook, & Lyons, 2011; Ray & Welsh, 2011) – the 'Beginning State Comfort Effect'. This drive towards considering the interaction needs of a partner in light of the shared task representation can extend to complex higher-order sequential action plans (Meyer, van der Wel, & Hunnius, 2013) and may be adjusted to the action capabilities of the partner, as well as the group and individual difficulty of the task (Ray, de Grosbois, & Welsh, 2017).

The Beginning State Comfort Effect, however, may not directly represent the facilitation of a co-agent's action as initially thought. Török et al. (2019) demonstrated that when transferring an object to a co-agent, the agent favoured co-efficient paths that minimized the aggregate costs of movement for the dyad rather than routes that minimized the costs for themselves or their co-agent. Thus, although accommodating another's action often looks altruistic, the effect could be better explained by the maximization of co-efficiency (Strachan & Török, 2020; Török et al., 2019; Török, Stanciu, Sebanz, & Csibra, 2022).

The present task was designed to conceptually mirror extractive foraging, which is commonly observed in wild chimpanzees (Hernandez-Aguilar, Moore, & Pickering, 2007) and orang-utans (Meulman & van Schaik, 2013); and all great apes (Mulcahy & Call, 2006) and capuchin monkeys (Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995) in the laboratory. The chimpanzee was provided with a stick which they needed to pass through a window to the experimenter who would then extract pieces of fruit from transparent tubes to give to the chimpanzee. Across several studies, we systematically investigated the extent to which chimpanzees incorporated a co-agent's action into their overall action plan.

## 2. Methods

The open access repository for this project can be found at: https://osf.io/txn6e/. At this address the data for all pre-tests and experiments is publicly accessible. Methods and written results for the pre-tests are also available at this location. The materials for the studies are physical and are thus not publicly available, however, collated example videos of the studies are publicly available at the above address.

### 2.1. Subjects

Twelve chimpanzees participated in this study (7 females and 5 males, mean age 29.6 years [SD = 13.3, range = 4–46 years, for individual demographic information please see supplementary materials] at the beginning of data collection). 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. The sample was obtained from two locations in order to maximise subjects. This sample size could be considered high given a recent systematic review indicating a median sample size of 9 for zoo-based primate cognition research (McEwen et al., 2022).

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. The zoos had slightly different testing environments, policies, and procedures: 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. If there was any potential for distraction the experiment coordinator (ESM) would provide juice to move the distracting chimpanzee to another part of the testing room away from the experimental set-up. It is possible that chimpanzees in Edinburgh may

have had greater secondary exposure to the experimental tasks, however, observing humans and chimpanzees passing objects to each other is relatively common at both locations.

Chimpanzees underwent two pre-tests before the experiment to determine if they would pass a stick to the experimenter and if they responded to gestural cues to pass a stick. If chimpanzees passed the stick on fewer than half of the trials in the first pre-test, they underwent training for passing a stick (see supplementary materials for further information).

### 2.2. Ethics

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 ethics committee at the University of St Andrews.

### 2.3. Apparatus

Chimpanzees were given the opportunity to approach a window (approximately 62 cm × 74 cm) which was either open mesh (Experiments 1, 2, 3B) or clear polycarbonate with two holes (approximately 4 cm in diameter, Experiments 3A, 4A, 4B) in their testing area. On the experimenter's side, 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 was set upon a table (see Fig. 1). A stick was required to retrieve the grape pieces by pushing them out of the tube, which could be done via either opening. The sticks used were an approximate length of 15 cm and were natural sticks from trees, similar to those which may be found in the chimpanzees' outdoor enclosure. In Experiment 1 (Hand Location Task), no additional materials were used. In Experiment 2 (Obstructed Hand Task), a handheld transceiver was placed in one hand. In Experiment 3 (Barrier Task), a three-sided, transparent polycarbonate barrier was placed on the experimenter's table and pushed against the testing window. The barrier was 50 cm tall, 37 cm wide (approximately half the width of the testing window) and was 32 cm away from the window. We piloted a shorter



**Fig. 1.** Chimpanzee (male, Velu) engaging in the handover task. Inset depicts the baited tubes. To retrieve the grape pieces the experimenter needed to insert the stick and push them out.

version of the barrier (21.5 cm 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. The open side was pushed against the testing window.

### 2.4. Procedure

Once a chimpanzee sat attentively in front of the testing window, the experimenter transferred a stick down a central plastic tube leading to the floor in front of the subject. After the chimpanzee was given the stick, the experimenter 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, the chimpanzee's name was used during the request to gain attention. Once the experimenter had grasped the stick (either with the hand closest to the passing location, or with their available hand (E1 and E2)), they used it to retrieve the pieces of grape for the chimpanzee using that hand (i.e., the side that the grape pieces were pushed from differed depending on the hand 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 inaccessible to the experimenter.

In Experiments 1 and 2, open hand locations were pseudo-randomized with no more than three of the same trial types in a row. In Experiments 3 and 4, a counterbalanced blocked design was used 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 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 the experimenter had held their hands in the mesh experiments.

In Experiment 3, the experimenter waited 5 s 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 it would take for the handover component to be completed 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. Experiment 3B was performed between Experiments 4A & 4B because 3B was a later addition to the already planned series of experiments. To summarise:

– Experiment 1 (Hand Location Task): Hand left side, centre, or right side behind mesh. For left and right location, the corresponding left and right hand were 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 left and one right) behind the mesh, palms facing one another. A handheld transceiver occupied one hand.
– Experiment 3 (Barrier Task): Transparent barrier obstructed one side of the window. Hands upward facing on left and right sides behind polycarbonate (3 A) or mesh (3B) window. Both hands were placed further back due to the presence of the barrier.
– Experiment 4 (Box Task): Opaque (4A) or transparent (4B) box prevented experimenter access to one hole in polycarbonate window. Hands facing upwards left and right sides behind window holes and box. With the opaque box, hands were raised so the box did not obstruct the chimpanzees' view of them. With the transparent box, hands were at the same height as the holes in the polycarbonate window and both hands were placed further back due to the presence of the box.

An example video of each experiment is in the supplementary

materials on the OSF.

# 3. Results

## 3.1. Data processing

All passing locations were manually coded from video recordings by the experimenter who collected data in Leipzig and oversaw data collection in Edinburgh (ESM). Importantly, data was coded on the initial location selection rather than final location selection because we took this to be reflective of 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, the data of the initial location was coded (see supplementary video for an example of such a location switch). In reality, location switches happened very rarely. No observations were excluded.

Windows that differed in terms of the spatial layout of the mesh were used. For appropriate data analysis, these needed to be equalized. Both types of mesh windows had ten squares along the vertical dimension. These were coded from 1 to 10 bottom to top. The mesh differed along the horizontal dimension: one type of window had 14 squares and the other 13. Because dividing the window into horizontal halves was necessary for this experiment, we 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 centre was accurately mapped between the windows. Therefore, a positive value represents a bias for the chimpanzee to pass to their right, and a negative value represents a bias for the chimpanzee to pass to their left.

A research assistant (blind to the first set of coding) 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). We evaluated consistency in coding using Cohen's $\kappa$ for judgements on the side selected in binary choices, and found a very high degree of consistency: $\kappa = 1$, $p < .001$. We 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 ICC $= 0.929$, p $< .001$, respectively.

We 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, Maechler, Bolker, & Walker, 2015). In all cases, we 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. We 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., 2019) and in cases in which the Variance Inflation Factor (VIF) exceeded 3, one of the collinear variables was removed (Johnston, Jones, & Manley, 2018). Effect sizes (odds ratios and Cohen's d) were calculated using the emmeans package (Lenth, Singmann, Love, Buerkner, & Herve, 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). We created all data visualisations using the ggplot2 package (Wickham, Chang, & Wickham, 2016). To account for slight differences in sizes of mesh and heights of holes between zoos, we included group (Edinburgh or Leipzig) in all models. We z-transformed the continuous variable 'trial' to normalise the data, and dummy-coded binomial variables as 0 and 1 to allow for clear comparisons.

## 3.2. Horizontal passing location

### 3.2.1. 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: $\chi2\ (2) = 74.82$, $p < .001$ ($d_{central\ hand} = 0.09$, $d_{left\ hand} = 0.82$, $d_{right\ hand} = 1.20$). No effect of trial was found: $\chi2\ (1) = 0.69$, $p = .41$ and no effect of group (Edinburgh or Leipzig): $\chi2\ (1) = 0.01$, $p = .94$. As can be seen in Fig. 2, when the hand was on the subject's left, the selected passing location was significantly further towards the left, and when the 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 the hand was presented.

### 3.2.2. Experiment 2 – Obstructed Hand Task

An LMM [pass location ~ occupied experimenter hand + trial + group + (1|subject)] revealed a significant shift in passing location towards the experimenter's free hand, or away from the experimenter's occupied hand (Fig. 2): $\chi2\ (1) = 17.22$, $p < .001$, $d = 0.71$. No effect of trial was found: $\chi2\ (1) = 3.41$, $p = .06$ and no effect of group (Edinburgh or Leipzig): $\chi2\ (1) = 0.32$, $p = .57$.

#### 3.2.2.1. 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: $\chi2\ (1) = 6.95$, $p = .008$, OR $= 3.52$; and no effect of group (Edinburgh or Leipzig): $\chi2\ (1) = 0.12$, $p = .73$. 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.

#### 3.2.2.2. Experiment 3B – Barrier Task (Mesh window).
Chimpanzees passed the stick further towards the unobstructed hand. An LMM [pass
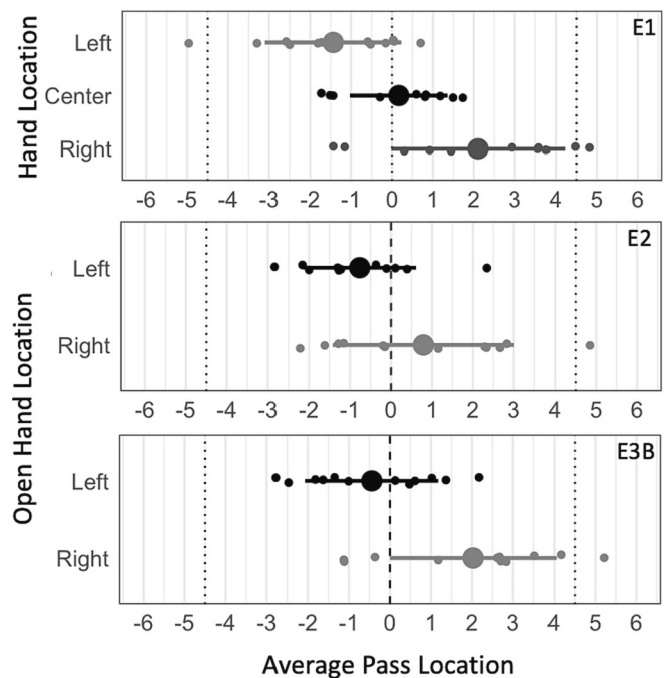


**Fig. 2.** Average horizontal passing location for Experiments 1, 2 and 3B as a function of the location of the experimenter's presented free hand. Large circles indicate the sample mean with error bars as standard deviation. Small circles represent each chimpanzee's mean. Dotted lines represent the 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 (dashed line).

location ~ barrier side + group + (1|subject)] showed a significant effect of barrier side on pass location: $\chi2 (1) = 40.97$, $p < .001$, $d = 1.15$. No effect of group was found (Edinburgh or Leipzig): $\chi2 (1) = 1.13$, $p = .29$. It is important to note that subjects participated in Experiment 3B after participating in Experiment 4 A. In Experiment 4 A, 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.

*3.2.2.3. 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: $\chi2 (1) = 130.45$, $p < .001$, $OR = 14.01$; and a significant main effect of group: $\chi2 (1) = 4.14$, $p = .04$; chimpanzees in the Edinburgh group had a greater overall tendency to pass to the right side. Subjects' passing side was affected by the location of the opaque box, and they were more likely to pass to the open side

*3.2.2.4. 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: $\chi2 (1) = 43.66$, $p < .001$, $OR = 3.04$; and no effect of group: $\chi2 (1) = 2.03$, $p = .15$. Subjects' passing side was affected by the location of the transparent box, and they were more likely to pass to the open side.

With both 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.

### 3.3. Vertical passing location

No difference in vertical passing locations was observed in any experiments for which this analysis was possible, that is, experiments with the mesh window, (Experiment 1: $\chi2 (2) = 0.32$, $p = .85$; Experiment 2: $\chi2 (1) = 0.59$, $p = .44$; Experiment 3B: $\chi2 (1) = 1.91$, $p = .17$).

For Experiment 3B, we looked at whether, when passing to the side which the barrier was on, chimpanzees passed higher to account for the obstruction to the experimenter's actions.[2] 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: $\chi2 (1) = 0.44$, $p = .51$; and no effect of group (Edinburgh or Leipzig): $\chi2 (1) = 0.30$, $p = .58$.

## 4. General discussion

Humans have a strong drive towards cooperating. Indeed, humans choose to engage in costly collaborative actions to achieve a goal over choosing to engage in solo action (Curioni et al., 2022). The present series of experiments investigated if chimpanzees' patterns of behaviour reflect human predispositions in handover tasks to comment on the potential for overlapping cognitive mechanisms in human and chimpanzee joint action cognition.

Experiment 1 showed that chimpanzees shifted their passing location towards the experimenter's hand in a joint handover-to-retrieve task, and Experiment 2 showed that passing was shifted towards an available hand and away from an occupied hand. Even with a binary choice that

required greater movement between the choice of an unobstructed or obstructed side (E3A), action adjustment was observed. When chimpanzees could choose any passing location (E3B), a shift towards the experimenter's unobstructed hand was also observed along the horizontal axis. Overall, the data demonstrates observable behavioural changes consistent with the notion that joint action efficiency is attended to or represented. Last, when human action was not possible at one location (E4A & E4B), a clear preference to pass to the side where there was the possibility of action was observed. In one experiment, the chimpanzees in Edinburgh demonstrated a rightward preference for passing. Given that this rightward preference is not consistent across experiments we caution against over-interpreting this effect.

Although the data are consistent with chimpanzees' possessing a cognitive system that understands the action demands of a co-actor and represents the actions required to meet a joint goal, the level of shared intention required is an open question. The chimpanzee may generate motor commands based on an internal model of the joint action without explicitly representing the notion of 'working together'. The co-agent is simply a 'social tool'(see Butterfill & Sinigaglia, 2014; Pacherie, 2013; Sinigaglia & Butterfill, 2022 for thorough discussions on cognition for joint action without the requirement of shared intention). At a very minimal level, if the chimpanzee represents the expected or desired action of their co-actor, their attention could be directed at the hand the co-agent would preferentially use, and their movements would then be shifted towards that hand as a by-product of attention. In humans, attention can be proactively driven by the script of the anticipated action (Land & Hayhoe, 2001) and what happens within the ocular motor system will directly influence what happens with the hands (Bekkering, Abrams, & Pratt, 1995; 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. However, in the binary choice situations which require greater action requirements of the chimpanzee, chimpanzees still selected the option that led to the free hand more frequently, suggesting more deliberate action selection.

The notion of generating joint action 'scripts' formed of multiple action representations that are linked together to meet a goal (Sinigaglia & Butterfill, 2022) may assist in explaining the differences between the experiments using opaque versus transparent obstructions. It may be more cognitively demanding to perceive a transparent object as an obstruction to action 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 to overcome the barrier would not be integrated into a sequential action plan as readily. Rather, a more accessible 'script' might be employed. Indeed, chimpanzees shifted the handover towards the unobstructed hand more when the obstruction was opaque than transparent in Experiment 4, although this shift occurred under both conditions.

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.

Direct familiarity with a partner's task could assist in strengthening any effects. The chimpanzees were engaging in a novel task with novel apparatus, thus, the information gained about their task partner's required actions were only gained via visual means which provides an incomplete picture. Indeed, human data shows that direct motor experience with a task leads to greater action accommodation (Ray et al., 2017) potentially via stronger action representations, suggesting that investigating familiarity both with the receiving component of the task and task partner could be an interesting line of inquiry.

The seeming 'action accommodation' within the present studies should not necessarily be considered a social process but rather as planning actions which are, on the whole, optimal (Wolpert & Miall,

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[2] This analysis was only possible for 7 of the 12 subjects as 5 subjects only passed to either the free side or barrier side.

1996) regardless of social context. This line of thought aligns well with theories of joint action based on human studies, which suggest that some mechanisms used in complex social situations are underpinned by very fundamental cognitive mechanisms that are not social in and of themselves. That is, the mechanisms discussed here could reflect general-purpose mechanisms that manifest in smooth social interactions.

Associative learning is commonly raised within the comparative literature (Heyes, 2012), and has also been raised pertaining to human joint action processes (Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2016; Heyes & Catmur, 2022). In the present work, chimpanzees' prior history of observing an open hand grasp an object may activate a motor plan to meet 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 such mechanisms in joint tasks is present in chimpanzees, aligning with patterns of behaviour observed in humans.

It should be noted that the frequency of tool handovers between chimpanzees to be used to retrieve a reward varies between experiments with zoo-housed chimpanzees. Whilst in some cases, chimpanzees readily pass tools to a conspecific requesting help (Yamamoto, Humle, & Tanaka, 2012), in other cases, this helping behaviour is rare (Nolte & Call, 2021). Nolte and Call (2021) suggest that differences between studies may be due to differences in paradigms. 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 and Call (2021) to conceive this 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 and 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. Given this species difference, it may be interesting to see how bonobos would perform in the current task.

Our results provide convergent evidence that chimpanzees, at least when they stand to gain something for themselves, represent the actions required in a joint task 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 result 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.

## CRediT authorship contribution statement

**Merryn D. Constable:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Emma Suvi McEwen:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Günther Knoblich:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing. **Callum Gibson:** Investigation, Resources. **Amanda Addison:** Investigation, Resources. **Sophia Nestor:** Investigation, Resources. **Josep Call:** Conceptualization, Funding acquisition, Methodology, Resources, Supervision,

Writing – review & editing.

## Data availability

Data is available on the OSF.

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