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The strategies used by chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*) to solve a simple coordination problem

Shona Duguid[a, b]*, Emily Wyman[c], Sebastian Grueneisen[b, d, e], and Michael Tomasello[b,f]

[a]School of Neuroscience and Psychology, University of St Andrews, UK
[b]Department of Developmental and Comparative Psychology,
Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[c] School of Economics, University of Nottingham, UK
[d] University of Michigan, Ann Arbor, USA
[e] Max Planck Institute for Human Development, Berlin, Germany
[f] Department of Psychology and Neuroscience, Duke University, USA

*Corresponding Author: shona.duguid@gmail.com ORCID: 0000-0003-4844-0673

Abstract

One of the challenges of collaboration is to coordinate decisions with others, and recent theories have proposed that humans in particular evolved skills to address this challenge. To test this hypothesis we compared the coordination abilities of 4 year old children and chimpanzees with a simple coordination problem. To retrieve a reward from a ‘puzzle box’ pairs of individuals were simply required to choose the same one of four options. If successful they each received the same reward, so there were no conflicts of interest. Individuals were paired with multiple partners over time. Both species were able to coordinate, but there were marked differences in the way they did so. Children were able to coordinate quickly and flexibly, adjusting easily to new partners, suggesting an understanding of the coordination process. In contrast, chimpanzees took time to converge on a single solution with each new partner, with no gains across partners, suggesting that their coordination was based only on repeating successful past choices. Together, these results support the hypothesis that humans have evolved unique skills for coordinating decisions and actions with others in the pursuit of common interests.

Keywords: cooperation; coordination; communication; chimpanzees; children

Introduction

It is the diversity, as well as the extent, of cooperation that is a distinguishing feature of the human species. Yet, the vast majority of research on cooperation focuses on the motivational challenges it presents for individuals, for example, how individuals overcome the temptation to free-ride on the efforts of others, or to defect altogether to do something more personally rewarding. Typically, the Prisoner's Dilemma, Public Goods Game, or other similar 'mixed motives' games in which there is a conflict of interest between the self and others, have been used to model these types of interactions (e.g. Fehr & Gaechter, 2000; Ostrom, 1998).

These games only represent part of human cooperation. Much of what humans do is mutualistic. By working together, we can produce or acquire benefits that would be unattainable for the individual. For example: hunting large game requires coordinated action of multiple individuals (e.g. Alvard & Nolin, 2002). If hunters fail to do their part the hunt fails and there are no benefits for anyone. Consequently, more research has recently focused on coordination games (see e.g. Balliet, Tybur, & Van Lange, 2017; Bardsley, Cubitt, et al., 2010; Grueneisen, Wyman, & Tomasello, 2014; Grueneisen, Wyman, & Tomasello, 2015a, 2015b; Mehta, Starmer, & Sugden, 1994a, 1994b; Parravano & Poulsen, 2015; Wyman, Rakoczy, & Tomasello, 2013) . These differ from mixed motives games in that individuals have matching interests and there are several ways of cooperating successfully. Individuals therefore do not have to choose between selfish and cooperative acts but instead have to collectively agree on one particular way of cooperating, e.g. which side of the road to drive on benefits everyone by reducing the likelihood of crashing into other drivers and maintaining the flow of traffic (Lewis, 1969; Schelling, 1960). Coordination games thus comprise a cognitive challenge, namely, to align one's decisions with others in the pursuit of common goals. This is not as trivial as it might seem. Since there can only be success if both partners choose the same solution, i.e. the decisions are highly interdependent, each individual only wants to choose a particular option if a partner does so too. This situation can potentially lead to paralysis, as each individual waits for the other to show her hand or otherwise commit to cooperation in a particular direction.

One especially interesting and important coordination situation for understanding the evolution of human cooperation is the stag hunt game. In this game individuals have the choice between a moderately rewarding option representing no risk ("hare") and a riskier but more rewarding option that can only be obtained via cooperation with a partner ("stag"). Consequently, the decision to cooperate comes with the risk of losing both options if a partner does not also choose to cooperate (Skyrms, 2004). How we play this game informs us about how we mitigate the risks of cooperation in the absence of potential cheaters (which is why it is also known as the assurance game). Tomasello and colleagues (Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012) argue that many of the unique features of human cognition and sociality evolved to meet the challenges of stag hunt type situations, especially in the context of collaborative foraging such as big game hunting when prey cannot be captured independently. For example, humans have highly distinctive forms of cooperative communication - the natural gestures of pointing and pantomiming, as well as conventional linguistic communication - might have evolved to overcome the challenges of coordinating (Tomasello, 2008, 2014). In the case of the stag hunt, communicating one's intentions, or providing a partner with information about the location of a “stag”, can facilitate the coordination of decisions to cooperate as well as to plan the specifics of the cooperation itself (see e.g. Thomas, DeScioli, Haque, & Pinker, 2014).

Support for this general proposal is provided by a recent study comparing how human children and their nearest great ape relatives, chimpanzees, coordinate decisions to cooperate. Duguid et al. (2014) presented pairs of four-year-old children and pairs of chimpanzees with two tasks with the overall structure of a stag hunt game. During the games, the participants could choose between collecting a relatively low value reward independently (e.g. cereal puffs) or working together by pulling two ends of a rope to release a higher value reward (e.g. gummibears).In the first version of the game, risks were low (the hare was of low value) and information was cheap (the partner's behavior was readily observable). In this case, partners of both species were able to coordinate successfully on the higher value stag more than 90% of the time, typically by one individual assuming all the risk and deciding to go for the stag unilaterally, with the other then following at basically no risk (a so-called leader-follower strategy; see Bullinger, Melis, & Tomasello, 2011). In contrast, when the risks were raised and observing the partner was more difficult, the chimpanzees became less successful, whereas the children compensated, and so remained highly successful, by communicating their intention to cooperate or information about the stag aimed at influencing the partner’s decision. Further studies with the stag hunt using different methods – token exchange and computer-based tasks - in which participants could explore the reward contingencies, also found that different primate species could sometimes find the best outcome of coordinating on the stag token, especially chimpanzees. However, only humans could do so reliably, particularly when they communicated about the task (Brosnan et al., 2011; Brosnan, Wilson, & Beran, 2012; Parrish, 2014).

There are many possible reasons for the different ways that chimpanzees and human children coordinate their decisions in stag hunt type situations, ranging from different skills of communication to different attitudes toward risk to different cognitive abilities. The issue is certainly not that chimpanzees cannot coordinate their actions with others at all; wild chimpanzees do this regularly in such activities as group hunting, border patrols, and inter-group conflicts, and coalitions in intragroup dominance contests (Watts & Mitani, 2002). Moreover, several experimental studies with captive chimpanzees have shown that they are able to coordinate their actions in order to acquire rewards which are inaccessible to individuals acting alone (e.g. (Chalmeau, 1994; Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2006). Coordination failure in chimpanzees thus does not appear to be related to difficulties in coordinating actions in time and space, but rather in coordinating their decisions with each other– a skill at which humans seemingly excel. This still leaves open many questions about the nature of the species difference.

One way to begin to identify the nature of the species difference in more detail is to present the two species with a novel but very simple pure coordination problem (Lewis, 1969; Schelling, 1960). In pure coordination games individuals will be successful if they both choose the same option out of several equally rewarding possibilities (and they do not have to risk any safe options to do so). The game is simple in the sense that all of the potential solutions to the problem are equal in value and in risk (unlike in the stag hunt). Unlike in the stag hunt, there is not one highly rewarding (and thus salient) option so players cannot succeed by choosing this obvious solution, assuming a partner will do the same; they have to find another way to converge on a solution. We might say that the coordination problem in the stag hunt game could be formulated as: “Will my partner choose the stag?” and in the pure coordination game as: “Which stag will my partner choose?” Formal mathematical theory struggles to explain how people generate solutions to such problems, but humans, including children, do surprisingly well at solving them without communication, based on such things as precedence (repeating previous solutions) and salience (using the unique solution; Bardsley, Mehta, Starmer, & Sugden, 2010; Camerer, 2003; Grueneisen et al., 2015a; Grueneisen, Wyman, & Tomasello, 2015).

Classically, coordination is difficult when the individuals cannot communicate or otherwise directly see what their potential partner is doing, and so they must find another way to create a "meeting of minds" (e.g., locating one another after a concert by both going to our shared car, because that is such an obvious thing for both of us to do). The simplest conceivable coordination situation is one in which both partners can see one another and are free to communicate as they are making their decisions. However, coordination problems in a broad sense frequently occur even with total informational access among partners. As an example, you may have experienced the situation in which you are walking towards another pedestrian on the footpath, and you have to decide whether you are both going left or right. Sometimes there is a little to-and-fro but in general this is a trivial problem for adults; however, this may not be the case for young children or chimpanzees. In the current study, therefore, we presented both chimpanzees (study 1) and young children (study 2) with a very simple coordination problem. To obtain rewards, two individuals each had to go to the same box, out of a row of four boxes, and press a button on their side. The pair had full visual access to one another and were free to communicate as they wished. Additionally, subjects did not have to press the buttons simultaneously but could do so sequentially, thus precise behavioral coordination was unnecessary. Our aim was to investigate the spontaneous strategies used to coordinate decisions so by reducing the behavioral coordination demands we allowed for the possibility of strategies such as a leader-follower strategy.

Our main measures of coordination success were a) the number of sessions until the criterion for reliable coordination was reached and b) how successful they were in the first session with each partner. Once coordinating reliably with their first partner, subjects were paired with new partners. If pairs were using a flexible strategy such as communicating about decisions then we would expect that changing partners would do little to hinder their coordination. Possibly they might profit from experience in the task with their first partner and be able to coordinate more quickly with subsequent partners. However, if they used simpler coordination strategies (e.g. always press the same button) then we would not expect an improvement across partners, and would expect coordination to drop in the first sessions with a new partner.

As an additional indicator of how they were solving the task we looked at how many of the buttons (i.e. how many of the possible solutions) they used to coordinate in a given session. In this case, our prediction was that a better understanding of the task and flexible coordinating strategy would allow pairs to use a greater range of solutions per session. Finally, we examined the strategies supporting reliable coordination: whether pairs were using a leader-follower strategy by waiting for a partner to choose first, and how they were using communication to coordinate. Overall, our main aim was to investigate whether, in the context of this simple coordination game, there would be species differences in coordination strategies that would indicate the cognitive or social-cognitive differences in coordination skills.

Study 1: Chimpanzee Coordination

Materials & Methods

Subjects

Sixteen chimpanzees (*Pan troglodytes*); six males and ten females were included in the final analyses (mean age= 21.4 years, range: 8-37 years, see supplementary materials for full subjects table). All subjects had extensive research experience with a wide range of experimental tasks. Seven additional subjects started the study but were not included in the final sample, either due to lack of motivation (*N*=2), because they consistently made more than one choice per trial (see procedure for further details; *N*=2), due to interference from a dependent offspring (N=1), or because their partner was excluded from the study (*N*= 2). Subjects were divided into two groups according to the social groups in which they were housed in (Group A, *N*=10; Group B, *N*=6). Partners were assigned pseudo-randomly according to the constraints of the study design. As individuals were in separate rooms during testing and food rewards were delivered directly to the respective rooms, tolerance was not a major concern, though individuals known to be intolerant were not paired together. Subjects could choose to stop participating at any time. All chimpanzees were housed at Wolfgang Köhler Primate Research Center, Leipzig Zoo, Germany. They were never food deprived and water was available *ad libitum* throughout testing.

Materials

Single-choice (training) box. The main feature of the single-choice apparatus was that it had two ‘buttons’ on either side. The apparatus was positioned in an alcove between two cages and one button could be accessed from each of the two adjacent cages (see ESM for schematic of set-up). The rest of the apparatus could only be accessed by the experimenter. It was constructed from PVC and Plexiglas. The buttons were actually the ends of solid plastic cylinders, which if pushed into the apparatus would move a lever and subsequently slide a horizontal Plexiglas panel towards the subject. The two panels associated with each of the buttons were lying on top of each other, covering a hole. If both buttons were pressed, the panels moved back, revealing the hole and any food items placed on top of the panels would fall down and become accessible to the subject. As long as one button had not yet been pressed the panels prevented the food from falling. Two larger semi-transparent panels (operated by the experimenters) could slide down in front of the two faces of the apparatus, blocking access to the buttons between trials.

Four-choice box. The four-choice box consisted of four single-button modules, so that four buttons (approx. 16cm apart.) could be accessed on either side of the apparatus (see Figure 1(a)). The whole box was 68x100x31cm. Each button module was associated with rewards (one piece for each subject per module). Only when both buttons on either side had been pressed was the food associated with those buttons released, one piece to either cage. Between trials the experimenter blocked access to the apparatus with semi-transparent panels covering the two faces of the apparatus accessible to the chimpanzees. When one choice was made, the remaining three were locked automatically by opaque plastic doors. Hence, only one choice could be made on each trial. After a choice was made all three doors associated with buttons that had not been pressed would lower. In contrast, the door associated with the button that had been chosen remained elevated, providing extra visual signals of which choice had been made. More than one button could be pressed simultaneously, thus increasing odds of success. Subjects that did this consistently were excluded from the study (*N*=2). Fifteen of the remaining subjects did occasionally press multiple buttons but did not use this strategy consistently (0.66% of all trials).

Procedure and Design

Training. Subjects completed four training phases to familiarise them with the task. All training was completed individually. Each phase was conducted on separate days.

The first three phases were with the single-choice apparatus. In Phase 1 subjects were paired with an experimenter, who pressed her button at the start of the trial. To access the food reward subjects were required to press the button on their side. Subjects proceeded to the next phase after acquiring the reward within one minute, on three consecutive trials (*M* =4.3 trials to pass, range 3-18).

Phase 2 used the same set-up but the experimenter either pressed her button as soon as the trial started (as in the previous phase), or five seconds after the subject. This was to draw attention to the fact that actions needed to be performed on both sides of the apparatus to gain access to the rewards. Subjects all received the same experience in this phase: four trials (two of each type) on either side of the apparatus (eight trials in total). Each side of the apparatus was conducted on a separate day.

During Phase 3 subjects had access to both sides of the single-choice apparatus (the door between the two rooms was open) and were required to acquire the food alone by pressing on both sides (within one minute on three consecutive trials; M=3.4 trials to completion, range 3-7).

Finally, subjects were familiarised with the four-choice box without rewards. They had one trial of up to five minutes to push a button on either side of the apparatus and to experience the locking mechanism.

Test trials. Subjects were presented with the four-choice apparatus in two conditions in a within-subjects design. In the *dyadic condition* subjects were tested in pairs. Each subject only had access to one side of the apparatus. Only when partners made corresponding choices would each receive one of the rewards associated with that choice. In the *solo condition* individual subjects had access to both sides of the apparatus and could retrieve both rewards associated with a button.

Before the trial began all four choices were baited with two food items. During baiting and re-setting between trials two large semi-transparent panels blocked access to the apparatus. Through this the chimpanzees could see that the experimenter was manipulating the apparatus but it was difficult to see exactly what the experimenter was doing (e.g. where re-baiting occurred). At the start of the trial the panels were removed by two experimenters. The trial ended when one choice had been made on either side, or three minutes had passed without a choice being made at which point the large panels were replaced. The buttons were re-set and the rewards replenished between each trial.

Each session consisted of 10 trials. Grapes were used as a reward for trials 1-5 and pellets (a higher-value food) for 6-10 to maintain motivation (if subjects did not press on a trial with grapes the next trial used pellets to increase motivation). If subjects did not press on three trials during a session, the session ended and continued on another day (this occurred on 24 occasions across all test sessions). Solo and dyadic test sessions differed only in whether subjects were tested alone (in which case the door between rooms was open to allow access to both sides of the apparatus) or in pairs (with one individual in each room).

Subjects were considered to have demonstrated coordination after pressing corresponding buttons significantly more often than chance on two consecutive sessions. The chance of both chimpanzees pressing a specific button, e.g. button 1, is 0.0625 (0.25*0.25) but since there are four sets of corresponding buttons (four potential solutions) the chance increases to 0.25 (0.0625*4). Thus, coordination was considered to be 6/10 successful trials (binomial test, $p<0.05$). However, as subjects initially seemed to be avoiding the button closest to the experimenter, a more conservative criterion of 7/10 on two consecutive sessions was applied (significantly above chance for a probability of success of 0.33); at the time of making this decision this button had been chosen in 4% of cases from a total of 390 trials with 7 pairs. The reason for the apparent avoidance is unclear as the button furthest from the experimenter was not the most common choice at this point and the avoidance was not as strong by the end of the experiment (see results section below). Pairs or individuals completed a maximum of 18 sessions.

Subjects were divided into two treatment groups that corresponded to the social groups in which they were housed. Members of group A were presented with the dyadic condition first. If they coordinated with their first partner, they were re-paired in a second round (with a partner that had also successfully coordinated with their previous partner) and, if successful, a third. Thus, individuals in group A had up to three partners before moving on to the solo condition. If they passed the solo condition, they returned to the dyadic condition for a maximum of two rounds. To investigate whether solving the problem individually first would improve subsequent coordination with a partner, group B started with the solo condition before moving on to the dyadic condition (with up to two partners due to the smaller number of individuals in the group). See ESM Table S1 for the full list of partners for each individual.

Dyads that successfully coordinated were shuffled to form new pairings. For Group A this was repeated so that each individual had up to three different partners prior to the solo condition. All individuals in Group A also took part in the solo condition regardless of their previous performance in the dyadic condition. Finally, those that successfully completed the solo condition went on to a second dyadic phase with new partners. For Group B all individuals completed the solo condition before those that were successful were paired for the dyadic condition. As far as possible pairs were formed from individuals that had shown preferences for different button numbers in their previous pairing (see results for further details).

Subjects were always on the same side of the box within a dyad (randomly assigned) but this was counterbalanced across dyads.

Refresher training. Between different test conditions subjects were given ‘refresher training’. This training was identical to phase 3 of training (including the pass criterion) and aimed to refresh their understanding that choices on both sides of the apparatus are necessary to retrieve the rewards.

Coding. All sessions were recorded using three digital cameras. For each trial the experimenter recorded the choice of each subject, and whether or not they were successful in retrieving the reward.

Analysis. To test the effect of condition on the number of sessions to successful coordination and the number of trials in the first sessions ending in success, we compared pairs with their first partner in group A with individual performances of members of group B in the solo condition with a Wilcoxon rank-sum test; thus, we compared independent samples while controlling for experience with the task. We used non-parametric survival analysis (Kaplan-Meier estimate of survival and log-rank test) to analyse the effect of group, partner number, or of passing the solo condition, on the number of sessions to success in the dyadic condition and the effect of group on the number of sessions to success in the solo condition, correcting for multiple testing where appropriate. This analysis takes into account the fact that testing was halted prior to some individuals/pairs coordinating successfully. We used non-parametric tests because the Cox models did not fulfil proportional hazards assumptions. We report medians (with 95% confidence intervals) based on the Kaplan-Meier estimate of survival for the number of sessions to pass criterion for coordination.

Generalised linear mixed models were employed to analyse the effects of group (condition order) and partner number on success in the first session in the dyadic condition, controlling for individual and pair identities. We used Generalised Liner Mixed Models (GLMMs; Baayen, Davidson, & Bates, 2008) with Poisson error structure for all analyses. Prior to inspection of the model results, we conducted an overall test of the full model (with all test and control variables) compared to the null model (the full model without test variables) using a likelihood ratio test. Only when this was significant did we consider the model results. The significance of test variables was tested individually using drop1 function of the lme4 package (using a likelihood ratio test). If the model included an interaction that was not found to contribute significantly to the model it was removed to produce a reduced model.

Finally, we used Fisher’s Exact test to analyse the distribution of preferred choices across buttons between conditions. Analysis was performed using R v3.0.1 (R Core Team, 2012), and the functions Surv and survfitt in the package survival; glmer in the package lme4; and CrossTable in the package gmodels. See supplementary materials for further details of the models.

Results and Discussion

Overall, the results show that chimpanzees are able to solve this coordination problem. With their first partner in the dyadic condition most pairs (7/8) could eventually coordinate reliably. This coordination success could be achieved in several different ways. One is by simply returning to a successful button, without any consideration of the behavior of their partner. Alternatively, with an understanding of the role of the partner, coordination could be achieved by responding to, predicting or influencing a partner's choices. To investigate this, we recombined pairs. If, through experience with the task, they had developed a flexible coordination strategy based on the decisions of themselves and their partner they should reach criterion more quickly with subsequent partners. We did not find evidence that pairs became quicker to coordinate with their new partners (*Mdn*=11 sessions, 95% CI [6, 18]; $\chi 2_4=2.1$, $p=0.71$, $N=23$; see Figure 2(a)). There were also no significant differences between pairs tested before completing the solo condition and those tested after passing the solo condition (comparing first partners only: $\chi 2_1=0$, $p=0.95$, $N=8$) nor between groups A and B ($\chi 2_1=0.7$, $p=0.40$, $N=23$). As a second measure of coordination success we analysed the number of successful trials in the first session and found no evidence of improvement in first session success across partners ($M= 3.0$, $SD= 2.7$; $\chi^2= 1.60$, $df= 2$, $p = .45$, $N=23$; see Figure 2(a)). In fact, success in the first sessions was very close to chance level (see Figure 2a; chance=2.5 trials).

The majority of chimpanzees (13/16) passed the solo condition. They were able to solve the task more quickly alone than in the dyadic condition (*Mdn solo*= 4; *Mdn dyadic*=10; $W=29$, $p<0.01$, $N=11$, *Mdn* difference=6.5, 95% CI [2, 10]) but there were no significant differences between conditions in first session success ($W=16.5$, $p=0.79$, $N=11$, *Mdn* difference=0.5, 95% CI [-7, 5]). There were also no differences between groups in the solo condition in either measure (number of sessions: *Mdn Group a* = 5.5, 95% CI [4, NA]; *Mdn Group b* =4.0, 95% CI [2, NA]; $\chi 2_1=2.4$, $p=0.12$, $N=16$; first session success: $\chi 2_2=2.4$, $p=0.30$, $N=16$). This difference between conditions indicated that coordinating with a partner created an additional challenge for the chimpanzees. It should be noted that the increase in sessions to success in dyadic condition is based on comparison between two separate social groups (housed in the same zoo with auditory and limited visual access to each other), so it is possible that group differences rather than experimental manipulation underlies this effect. However, we did not have any a priori expectations for differences in performance between groups and we did not find any significant differences in our main measures, increasing our confidence that this is a condition effect. Each of the four possible solutions to the task (i.e. each set of buttons) resulted in an equal value of reward; thus, if partners were coordinating flexibly with their partner they could potentially coordinate on the whole range of solutions. However, pairs tended to converge on one single set of buttons ($M=1.21$ sets per session per pair, $SD=0.22$), presumably by choosing the option that had previously led to success. One possible explanation for this is that one set of buttons was perceptually salient and thus attracted the attention of both individuals to it, leading them to choose this preferentially and consequently to coordinate. In contradiction to this explanation, there was no indication of a clearly preferred option overall: there was some evidence of avoidance of the button closest to the experimenter (representing 12% choices) but choices were distributed evenly across the remaining three boxes (representing 28-31% choices each). We used this variation across pairs to reduce the likelihood of pairs coordinating by chance: each new pairing, as far as possible, was made up of individuals who had coordinated on a different set of buttons in the previous round. Thus, in achieving coordination with new partners, chimpanzees did show some flexibility.

Individuals in the solo condition also generally used one set of buttons (M=1.33 set per session per pair, SD=0.25), but the distribution of choices differed to that of the dyadic condition ($\chi 2_3$=191.33, p<0.01, N=7086). The pattern suggests that each pair converges on one set of buttons (and this differed between pairs). This results in successful but somewhat inflexible coordination, as new solutions to the problem need to be re-established with new partners.

Chimpanzees were able to coordinate but solving the task with a partner seemed to make it significantly more difficult for them in comparison to solving the task alone. In study 2 we investigated whether this was the case for 4 year old children.

Study 2: Children's coordination

In the second study we investigated how young children would solve the same coordination problem. Our aim was to reproduce the basic structure and logic of the chimpanzee study as closely as possible to be able to compare coordination strategies. The main exception was that young children cannot do so many trials, and so we reduced our sessions to five trials each.

Materials & Methods

Subjects

Forty 4 year old children were included in the final analyses; 20 boys and 20 girls (M_{age}=50.8 months, range =48-54 months). We chose 4 year olds to provide a comparison to a previous coordination game also played by 4 year old children and chimpanzees (Duguid et al., 2014). Additionally, pilot testing indicated that this was the youngest age that they reliably engaged in the task. They were paired in 47 dyads, with each child tested with up to 3 different partners. Both children in the dyad were from the same kindergarten, but not necessarily the same class (26 dyads from the same class and 21 from different classes). In order to maximise the number of potential dyads children were paired with same and different sex partners (mixed-sex = 29 dyads, female = 9 dyads, and male = 9 dyads). A further 11 children completed the training but were not included in the final sample either because there was no partner available for them (i.e. there was an odd number of children at a particular kindergarten, *N*=3 children), or because they were not available to complete the required number of sessions with their first partner (*N*= 8 children). All testing took place at kindergartens in the Leipzig city area, Germany; the children were recruited from a database of parents who volunteered to take part in child development studies.

Materials

The design and size of the single-choice (training) box and four-choice box were identical to study 1, with the exception of lighter building materials (e.g. wood) and some painting to make the task more appealing to the children (see Figure 1(b)). The children's apparatus also included two large red cardboard barriers to occlude the apparatus between trials (similar to the large panels used in the ape apparatus). Additionally, rather than food rewards, children could release two red wooden balls by pressing the corresponding buttons. These balls could be used to produce music from a "pling machine" by rolling the balls down a tube on the machine (this reward method has been used successfully in a number of previous studies, e.g. Moore, Mueller, Kaminski, & Tomasello, 2015; Rakoczy, Grafenhain, Cluver, Dalhoff, & Sternkopf, 2014; Wobber, Herrmann, Hare, Wrangham, & Tomasello, 2014).

Procedure and Design

Training. The first experimenter introduced herself during a short warm-up phase and engaged the child in conversation before starting the training. A second experimenter operated and reset the apparatuses but most of the interaction was with the first experimenter to reduce the likelihood that children would engage the second experimenter during the task. Children completed the same four training phases as the chimpanzees. They were trained individually and completed all phases in one session in order to reduce the total number of testing days. One additional trial with the single-choice box was added to the end of the children's training so that the session would end with a positive experience.

To keep the training as comparable as possible, the experimenter used minimal verbal instructions. Most importantly, the experimenter did not explain how the box worked so that the children would not have information about the mechanism unavailable to the chimpanzees. This included not referring to the different choices as buttons.

Test trials. As in study 1 participants were presented with the four-choice apparatus in two conditions in a within-subjects design. In the *dyadic condition* children were tested in pairs, with each subject having access to one side of the apparatus. In the *solo condition* individual subjects had access to both sides of the apparatus, and could retrieve both rewards associated with a button by making corresponding choices on either side.

The procedure for test trials was very similar to the chimpanzees'. Before the trial began all four choices were baited with two balls. At the start of the trial the second experimenter removed the panels so that the subject(s) had access to the buttons. The trial ended when one choice had been made on either side, at which point the panels were replaced. The buttons were re-set and the rewards replenished between each trial.

Children were given sessions of 5 trials (in contrast to the 10 trials for chimpanzees), and up to 5 sessions (25 trials) on the same day to reduce the total number of testing days. The first test session was on the same day as the training. They were tested with a single partner on any given day. Dyads were considered to be successfully coordinating after pressing corresponding buttons on 4/5 trials in two consecutive sessions (binomial test, $p<0.05$) and completed a maximum of 8 sessions (40 trials). This performance criterion (4/5 successful trials) was significantly above chance at a probability of success of both 0.25 and 0.33, thus this criterion was as conservative as that used for chimpanzees (probability of success = 0.33). The solo condition consisted of two sessions of five trials. Again, at least 4/5 correct in both blocks was considered successful.

All children were tested with up to three partners in the dyadic condition. In contrast to the chimpanzees they were always tested in the solo condition after completing the dyadic condition. As in study 1, pairs that successfully coordinated were re-shuffled. Only children who successfully coordinated with a first partner were paired with a second partner and third partner. In some cases, children were not available, or a partner was not available to be tested with a second or third partner. In total 19 dyads were first partners; 18 dyads were second partners; and 10 dyads were third partners. As far as possible, chimpanzees were shuffled in a way that would minimise the likelihood that new partners would coordinate by chance by pairing individuals that had converged on different buttons with previous partners. This was not possible for child dyads as they did not show the same pattern of convergence (see section 3.2). As many subjects as possible were tested in the solo condition, after completing the dyadic condition (*N* children tested after first partner=4, second partner =11, third partner =14).

Coding. In addition to coding all decisions (as in Study 1), in order to get a better understanding of how pairs were coordinating in the dyadic condition, a subset of sessions from successful dyads of both children and chimpanzees were coded in more detail. For the two sessions in which pairs reached criterion and, if applicable, the two preceding this, we recorded the time between partners pushing as well as communication for both species.

The timing of decisions were categorised as simultaneous (≤1s between decisions of both partners) or sequential (>1s between decisions). To characterise the communication within dyads we were interested whether they a) used attention-getters to direct a partner's attention to the task, e.g. calling their name or, for the apes using noisy gestures such as knocking on the panel between them and their partner, and b) whether they referred to a specific box, e.g. by pointing to a button, or saying "here" or "this one". Only communication that occurred during the trial was coded (from when the barriers were lifted until both individuals had made their decision).

Reliability. A second coder, blind to the hypotheses, coded four of the successful pairs of chimpanzees and eight of the successful pairs of children for which box was chosen ($K_{\text{chimpanzees}}$=1.00; K_{children}=1.00), timing of decisions (simultaneous or sequential; $K_{\text{chimpanzees}}$=0.94; K_{children}=0.97), and communication events ($K_{\text{chimpanzees}}$=0.99; K_{children}=0.97) and type ($K_{\text{chimpanzees}}$=1.00; K_{children}=0.92). For events that occurred very infrequently (communication in chimpanzees) we calculated a prevalence-adjusted bias-adjusted kappa (Byrt, Bishop & Carlin, 1993).

Analysis. The main analyses were performed as in Study 1 for comparability: non-parametric survival analysis to test the effects of partner number, gender (girls, boys or mixed pairs), and whether they were in the same kindergarten class on the number of sessions to successful coordination. GLMM's were used to test the effects of the same predictors on coordination success in the first session. To compare independent samples of first session success in the dyadic condition to the solo condition, we compared pairs tested with a third partner to individuals tested in the solo condition after their second partner using a Wilcoxin rank-sum test. Since all children completed the solo condition only after the dyadic condition this was the best comparison to the chimpanzees' data that controlled for experience (see ESM for further details).

In addition, GLMM's were used to analyse species differences in the timing of decisions (simultaneous or sequential) and communication. To run these analyses we used the subset of sessions coded for the relative timing of both partner's decisions and communication between partners during the trial. In both full models we included as test variables: species and session success (whether the session was one of the two above criterion, or the two prior to that), partner number as a control variable; and the random effects: identity of the pair, and the identity of each of the individuals in the pair.

Results and Discussion

Children's Coordination

The four year old children were very successful at coordinating in this task. This was already evident with their first partner. All 19 of the initial pairings reached criterion and did so very quickly (*Mdn*= 3 sessions, 95% CI [2, 3]). The picture was similar with second and third partners (see Figure 2(b)). With their second partner most pairs reached criterion (16 of 18), and in a median of 2 sessions (the minimum possible, 95% CI [2, 4]). With their third partner all pairs were successful (10/10; *Mdn* = 2 sessions, 95% CI [2, NA]). Overall, the number of sessions required to coordination reliably did not decrease significantly with the number of partners, though there was a trend in this direction ($\chi 2_2$=5.4, *p*=0.068, *N*=47); this may be because the children were reaching the criterion so quickly from the onset. There was significant improvement in first session success across partners (estimate±s.e.= 0.24±0.10; χ^2= 5.26*, df*= 1*, p*=0.02, *N*=47*,* see Figure 2(b)). There were no significant effects of the sex of the dyad or whether they were form the same kindergarten class on either measure of performance.

Pairs of children were coordinating on a wide range of solutions within each session: about two-thirds of pairs were using three or four sets of buttons within a session (*M* =1.94 buttons used per session per dyad, *SD*=0.94). As there were only five trials per session, this meant that for many pairs their coordination was flexible enough to switch between buttons on almost every trial. However, a significant number of pairs were also very similar to the chimpanzees: converging on one or two buttons.

Children were also very successful in the solo condition. Due to time constraints the solo condition was restricted to two sessions, and they either passed immediately (>4/5 on both sessions) or failed. The majority of children passed within these two sessions (24 of 29). A comparison of performance in the first session between solo and dyadic conditions shows no significant difference (W=57, p=0.90, N=21, *Mdn* difference<0.01, 95% CI [-1, 1]).). This suggests that coordinating with a partner was no more difficult than completing the task independently.

Comparison of coordination between children and chimpanzees

A more detailed analysis of successful coordination in both species suggests two ways in which children's coordination differed from the chimpanzees. We compared the behaviour of the chimpanzees in Study 1 to the children in Study 2. The relative timing of decisions indicates the first way in which coordination differed, in this context. One way to solve this coordination problem is a leader-follower strategy: one partner waits for the other to act first and then follows her lead. This is particularly efficient in situations with complete visual access and abundant time to make decisions such as the current task. We compared the proportion of decisions that were made simultaneously (within 1s of each other) with those that were sequential (>1s between decisions), with the assumption that increased time between decisions allows for the possibility of a leader-follower strategy. In the majority of trials children made sequential decisions, more so than chimpanzees ($M_{children}$=72.85% sequential decisions per dyad, SD= 22.93; $M_{chimpanzees}$=43.99%, SE=27.70; estimate±s.e.= -1.50±0.44; χ^2= 10.36, df= 1, p<0.01, N=1227 trials). This is consistent with the idea that children were following a partner's decision. It would also explain how some children (N=5) did not perform above chance in the solo condition but were successful in the dyadic condition: as long as one individual can wait for their partner to initiate, they can follow.

A second way to coordinate is to communicate decisions to a partner. Children were more likely to communicate to each other about the task (via gestures or vocalisation) than chimpanzees were ($M_{children}$=26.22% trials per dyad, SD= 33.46; $M_{chimpanzees}$=3.12%, SD=5.10; estimate±s.e.= 2.69±0.90; χ^2= 8.01, df= 1, p<0.01, N=1227 trials). In most cases this included a verbal and/or gestural reference to a specific choice, e.g. saying "here" while pointing to the button they had/were about to choose (78.10% trials with communication included an act of reference to a specific choice), rather than more general attention-getters such as calling their partner's name. Children often communicated before either of them had made their decision

(54.01% trials with communication were pre-decision). This is different from the type of communication observed with the chimpanzees: in the few instances in which they did communicate they used gestural attention-getters, but did not refer to specific choices. Typically, this involved a noisy gesture towards a partner (e.g. knocking in the wire mesh between the cages) while waiting for them to make their decision after having already made their own choice. We reduced the likelihood of coding signs of general frustration with the task by coding gestures directed towards the partner, however, to better determine whether the behaviours we observed were intended to solicit action from the partner, we would need an additional version of the task in which communication was not possible.

While children do communicate substantially more often than chimpanzees in this situation, 40% of pairs did not communicate about the task. Despite the lack of verbal or gestural communication, they were still highly successful at coordinating their decisions. This highlights an important point that language may be a very useful tool, not only for coordination (see e.g. Dean, Kendal, Schapiro, Thierry, & Laland, 2012) but it is not the only tool available for coordinating with others and it is likely that a suite of socio-cognitive capacities support human collaboration.

General Discussion

The results of the two studies demonstrate that children and chimpanzees used very different strategies to solve the same coordination problem. Chimpanzees took many sessions to converge on a successful solution with each partner, and less successfully than in an individual version of the task. Children were already efficient at coordinating with their first partner, but still showed signs of improvement with further partners. Children were able to use the range of possible solutions (sets of buttons) flexibly by using a leader-follower strategy and communication to inform or direct partners towards a set of buttons.

Our results extend previous findings showing that four year old children are able to cooperate and coordinate decisions when there is a salient optimal solution for both partners (Duguid et al., 2014; Wyman et al., 2013). In the current task all options were of equal value, perceptually similar and visible to both players so to coordinate effectively participants had to take each other’s decisions into account and adjust their own accordingly. At 4 years old, children are efficient at solving the coordination problem with peers in an interactive context where they are able to see each other and communicate freely. This ability makes way for the capacity to coordinate with absent partners (when no communication is possible) at the age of 5 or 6 using skills such as second-order theory of mind or cultural common ground (Goldvicht-Bacon & Diesendruck, 2016; Grueneisen et al., 2015a; Grueneisen et al., 2015b).

It is clear that communication can be used to solve coordination problems like the one presented here: by pointing out one of the four buttons individuals can make their intentions clear so that there is no longer a dilemma for their partner. We see that the children do make use of verbal and gestural communication for this purpose. However, it is also interesting to note that they only do so in about 25% trials, and 40% of pairs did not communicate at all. This strongly suggests that explicit communication may be an important tool for solving the problem but it is not the only way in which they can coordinate. These pairs may have simple strategies to coordinate, for example, they were successful once and simply continued to make the same choice or followed the choices of a naïve leader. Research with adults suggests that they will make their choices, or the movements of instrumental actions, more predictable to facilitate coordination (e.g. Mehta et al., 1994a; Vesper, van der Wel, Knoblich, & Sebanz, 2011). It possible that the children in this study were also using more subtle forms of communication. The right kind of eye contact from an adult experimenter can facilitate cooperation in children of similar ages in the stag hunt game (Siposova, Tomasello, & Carpenter, 2018; Wyman et al., 2013) and we observed children making choices in predictable patterns (e.g. going from one end of the box to the other). However, we would need further investigation to formulate and test specific hypotheses of how these more subtle types of communication could facilitate coordination in the current context in which dyads need to coordinate between multiple equivalent options. For example, with versions of the task in which children cannot communicate at all, or only visually, we would expect reduced ability to coordinate successfully, or for children to rely on less flexible strategies such as converging on one choice by chance.

The overall pattern of coordination was qualitatively different for the chimpanzees: as well as taking several sessions to reach criterion they did not quickly adapt to new partners, converging to a single set of buttons rather than flexibly switching between them. One explanation for this pattern is that individuals simply return to successful buttons without any consideration of their partner's actions. This explains the time required to establish reliable coordination, but it is efficient once achieved. It is not possible to rule out this strategy, however, two findings suggest that this does not completely account for their decisions. The first is that individuals were quicker to solve the task alone than with a partner, indicating that coordinating with a partner is an additional challenge but one that many of them did eventually succeed in. Secondly, chimpanzees did communicate with attention-getters to engage a partner while waiting for their partners to choose, indicating an understanding that the partner's action is necessary. This form of communication is similar to the way chimpanzees have communicated in previous experimental situations in which they required help from conspecifics e.g. (Yamamoto, Humle, & Tanaka, 2012; Yamamoto & Tanaka, 2009). Our evidence suggests that, chimpanzees in this task do take into account that a partner needs to act but not which actions a partner takes within a test trial. Once pairs discover a successful solution, they can maintain success with the same partner without communicating or even monitoring their decisions.

Previously, Bullinger et al. (2011) suggested that chimpanzees were using a leader-follower strategy, to coordinate their decisions in a stag hunt coordination problem. This strategy could account for the condition differences in the present coordination problem: when operating the puzzle-box alone, their actions were always sequential so the information about their own choice was always available. However, in the dyadic condition this did not appear be the main strategy, individuals did not wait for information about their partner's choice. In other cooperative tasks chimpanzees have shown that they are capable of waiting in order to work together (e.g. the 'loose string' task; (Hirata & Fuwa, 2007; Melis et al., 2006; Melis, Hare, & Tomasello, 2009). These studies, however, have included training during which individuals learn that any action before the arrival of a partner results in task failure. In the current set up, waiting only provides useful information about a partner's decision but is not necessary to operate the puzzle box successfully. Although apes have been shown to inhibit choices to seek information actively in non-social contexts (e.g. Bohn, Allritz, Call, & Völter, 2017; Call, 2010), evidence from cooperative tasks suggests that this may be more difficult in social contexts (Bullinger, Melis, & Tomasello, 2014 and the current study). Further studies would be necessary to determine whether factors such as task complexity, inhibition or metacognitive skills contribute to this apparent difficulty. Another difference between the current task and that of tasks like Bullinger et al. (2011), and more recently Melis & Tomasello (2019), that would make a leader follower strategy more challenging is that the dimensions of the apparatus preclude the use of body position of the partner to indicate a choice. Instead the chimpanzees have to focus on manual actions or gestures, or the apparatus itself, which may be less salient signals.

Investigating the proximate mechanisms of human and chimpanzee collaboration in a mutualistic context is key to fully understanding the evolution of human cooperation (Balliet, Tybur, & Lange; Balliet et al., 2017; Tomasello, 2016) and our results contribute to the developing picture of the way chimpanzees and children coordinate their decisions. In previous experiments where the costs of coordination failure were low and there was a salient, high value choice both chimpanzees and children were very successful at coordinating their actions with a partner (Hirata & Fuwa, 2007; Melis et al., 2006; Melis et al., 2009; Wyman et al., 2013). However, when the costs increase (Duguid et al., 2014) and when efficient coordination requires coordination of decisions (such as in the current task) humans seem to excel. The way in which communication is used by both species indicates significant differences in their coordination strategies: children are engaging with their peers to solve the problem together even before making any choices, while chimpanzees seem to solve the problem more individualistically. The current task was designed specifically to investigate coordination when it is difficult to make predictions about a partner's behaviour (because all the options are of equal value and effort). However, to understand how chimpanzees coordinate decisions during activities such as group hunting or decisions about travel directions, another essential avenue of research will be to examine whether chimpanzees use the same socio-cognitive abilities shown in competitive tasks to predict conspecific behaviour in cooperative contexts and coordinate with them (e.g. Grueneisen, Duguid, Saur, & Tomasello, 2017; Karg, Schmelz, Call, & Tomasello, 2015). If these abilities are context-specific we can gain a clearer picture of the of proximate mechanisms underlying coordination in chimpanzees as well the evolutionary history of human cooperation. Overall, the current results are consistent with the view that humans have evolved socio-cognitive skills supporting the ability to coordinate decisions effectively in the context of mutualistic collaboration.

Ethics Statement

All the experiments in this study were approved by an internal ethics committee at the Max Planck Institute for Evolutionary Anthropology. Research was non-invasive and strictly adhered to the legal requirements of Germany. Animal husbandry and research comply with the EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria and the WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquarium.

Data Availability

The data are available as supplementary material associated with the manuscript.

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Competing interests

We have no competing interests.

Author contributions

SD, EW, SG & MT designed the study and commented on the manuscript; SD also collected and analyzed data and drafted the manuscript.

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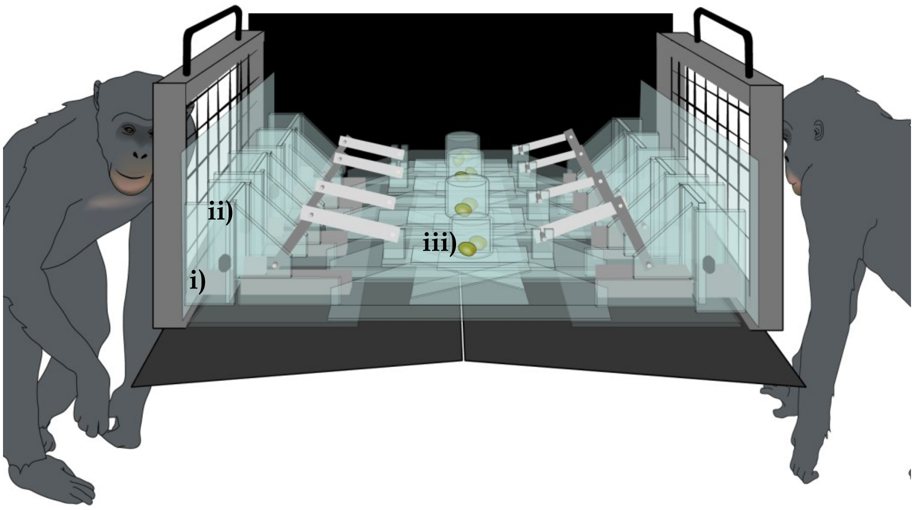
a)



b)

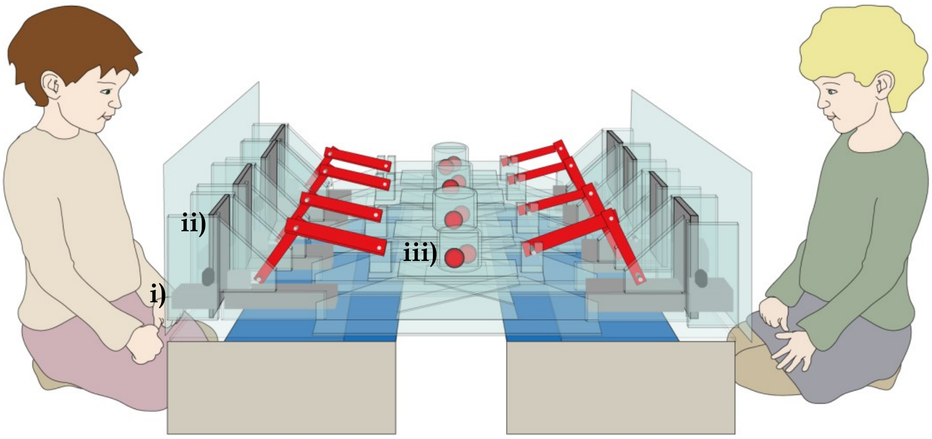


Figure 1. Experimental set-up in dyadic condition for (a) chimpanzees and (b) 4-year old children. In the solo condition individual participants were able to move around the puzzle-box. i) One of the ‘buttons’ available to the participants; ii) the sliding doors that lock the remaining choices after one button has been pressed; iii) the rewards, one for each partner.

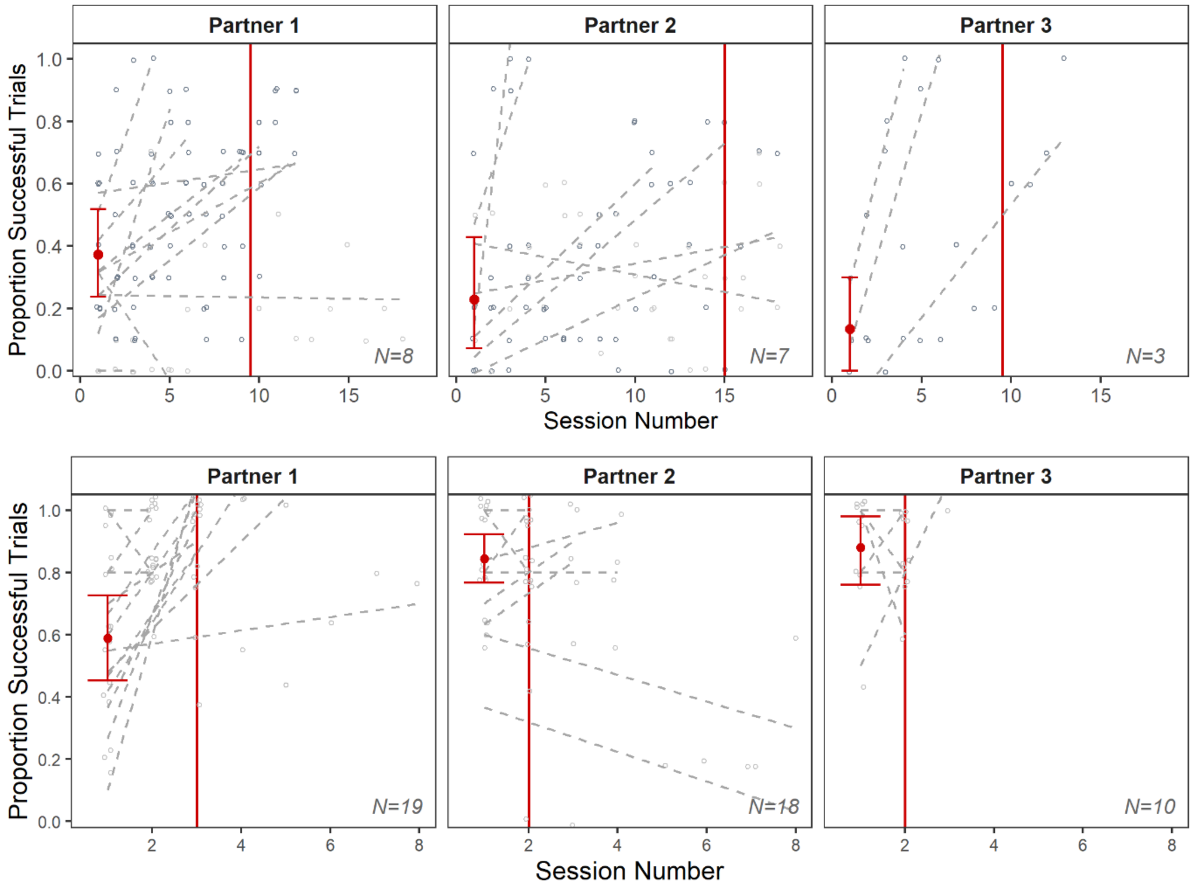


Figure 2. Coordination success across sessions for chimpanzees (a) and children (b) for partner numbers 1-3. The red vertical line indicates the median number of sessions to reach criterion. The red point (+ 95% CI) indicates the mean success in session 1. Each pair tested is represented by a dashed line.