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

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10 Shona Duguid^{a, b*}, Emily Wyman^c, Sebastian Grueneisen^{b, d, e}, and Michael Tomasello^{b, f}

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12
13 ^aSchool of Neuroscience and Psychology, University of St Andrews, UK

14 ^bDepartment of Developmental and Comparative Psychology,
15 Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

16 ^c School of Economics, University of Nottingham, UK

17 ^d University of Michigan, Ann Arbor, USA

18 ^e Max Planck Institute for Human Development, Berlin, Germany

19 ^fDepartment of Psychology and Neuroscience, Duke University, USA
20

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

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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

69 both options if a partner does not also choose to cooperate (Skyrms, 2004). How we play this game informs us
70 about how we mitigate the risks of cooperation in the absence of potential cheaters (which is why it is also
71 known as the assurance game). Tomasello and colleagues (Tomasello, Melis, Tennie, Wyman, & Herrmann,
72 2012) argue that many of the unique features of human cognition and sociality evolved to meet the challenges of
73 stag hunt type situations, especially in the context of collaborative foraging such as big game hunting when prey
74 cannot be captured independently. For example, humans have highly distinctive forms of cooperative
75 communication - the natural gestures of pointing and pantomiming, as well as conventional linguistic
76 communication - might have evolved to overcome the challenges of coordinating (Tomasello, 2008, 2014). In
77 the case of the stag hunt, communicating one's intentions, or providing a partner with information about the
78 location of a "stag", can facilitate the coordination of decisions to cooperate as well as to plan the specifics of
79 the cooperation itself (see e.g. Thomas, DeScioli, Haque, & Pinker, 2014).

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

98 There are many possible reasons for the different ways that chimpanzees and human children
99 coordinate their decisions in stag hunt type situations, ranging from different skills of communication to
100 different attitudes toward risk to different cognitive abilities. The issue is certainly not that chimpanzees cannot
101 coordinate their actions with others at all; wild chimpanzees do this regularly in such activities as group hunting,
102 border patrols, and inter-group conflicts, and coalitions in intragroup dominance contests (Watts & Mitani,
103 2002). Moreover, several experimental studies with captive chimpanzees have shown that they are able to
104 coordinate their actions in order to acquire rewards which are inaccessible to individuals acting alone (e.g.
105 (Chalmeau, 1994; Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2006). Coordination failure in chimpanzees
106 thus does not appear to be related to difficulties in coordinating actions in time and space, but rather in
107 coordinating their decisions with each other— a skill at which humans seemingly excel. This still leaves open
108 many questions about the nature of the species difference.

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

122 Classically, coordination is difficult when the individuals cannot communicate or otherwise directly see
123 what their potential partner is doing, and so they must find another way to create a "meeting of minds" (e.g.,
124 locating one another after a concert by both going to our shared car, because that is such an obvious thing for
125 both of us to do). The simplest conceivable coordination situation is one in which both partners can see one
126 another and are free to communicate as they are making their decisions. However, coordination problems in a

127 broad sense frequently occur even with total informational access among partners. As an example, you may
128 have experienced the situation in which you are walking towards another pedestrian on the footpath, and you
129 have to decide whether you are both going left or right. Sometimes there is a little to-and-fro but in general this
130 is a trivial problem for adults; however, this may not be the case for young children or chimpanzees. In the
131 current study, therefore, we presented both chimpanzees (study 1) and young children (study 2) with a very
132 simple coordination problem. To obtain rewards, two individuals each had to go to the same box, out of a row of
133 four boxes, and press a button on their side. The pair had full visual access to one another and were free to
134 communicate as they wished. Additionally, subjects did not have to press the buttons simultaneously but could
135 do so sequentially, thus precise behavioral coordination was unnecessary. Our aim was to investigate the
136 spontaneous strategies used to coordinate decisions so by reducing the behavioral coordination demands we
137 allowed for the possibility of strategies such as a leader-follower strategy.

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

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

154

155

Study 1: Chimpanzee Coordination

156

157 **Materials & Methods**158 **Subjects**

159 Sixteen chimpanzees (*Pan troglodytes*); six males and ten females were included in the final analyses
160 (mean age= 21.4 years, range: 8-37 years, see supplementary materials for full subjects table). All subjects had
161 extensive research experience with a wide range of experimental tasks. Seven additional subjects started the
162 study but were not included in the final sample, either due to lack of motivation ($N=2$), because they
163 consistently made more than one choice per trial (see procedure for further details; $N=2$), due to interference
164 from a dependent offspring ($N=1$), or because their partner was excluded from the study ($N=2$). Subjects were
165 divided into two groups according to the social groups in which they were housed in (Group A, $N=10$; Group B,
166 $N=6$). Partners were assigned pseudo-randomly according to the constraints of the study design. As individuals
167 were in separate rooms during testing and food rewards were delivered directly to the respective rooms,
168 tolerance was not a major concern, though individuals known to be intolerant were not paired together. Subjects
169 could choose to stop participating at any time. All chimpanzees were housed at Wolfgang Köhler Primate
170 Research Center, Leipzig Zoo, Germany. They were never food deprived and water was available *ad libitum*
171 throughout testing.

172

173 **Materials**

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

183 (operated by the experimenters) could slide down in front of the two faces of the apparatus, blocking access to
184 the buttons between trials.

185 **Four-choice box.** The four-choice box consisted of four single-button modules, so that four buttons
186 (approx. 16cm apart.) could be accessed on either side of the apparatus (see Figure 1(a)). The whole box was
187 68x100x31cm. Each button module was associated with rewards (one piece for each subject per module). Only
188 when both buttons on either side had been pressed was the food associated with those buttons released, one
189 piece to either cage. Between trials the experimenter blocked access to the apparatus with semi-transparent
190 panels covering the two faces of the apparatus accessible to the chimpanzees. When one choice was made, the
191 remaining three were locked automatically by opaque plastic doors. Hence, only one choice could be made on
192 each trial. After a choice was made all three doors associated with buttons that had not been pressed would
193 lower. In contrast, the door associated with the button that had been chosen remained elevated, providing extra
194 visual signals of which choice had been made. More than one button could be pressed simultaneously, thus
195 increasing odds of success. Subjects that did this consistently were excluded from the study ($N=2$). Fifteen of
196 the remaining subjects did occasionally press multiple buttons but did not use this strategy consistently (0.66%
197 of all trials).

198

199 **Procedure and Design**

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

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

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

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

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

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

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

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

234 Subjects were considered to have demonstrated coordination after pressing corresponding buttons
 235 significantly more often than chance on two consecutive sessions. The chance of both chimpanzees pressing a
 236 specific button, e.g. button 1, is 0.0625 ($0.25*0.25$) but since there are four sets of corresponding buttons (four
 237 potential solutions) the chance increases to 0.25 ($0.0625*4$). Thus, coordination was considered to be 6/10
 238 successful trials (binomial test, $p<0.05$). However, as subjects initially seemed to be avoiding the button closest
 239 to the experimenter, a more conservative criterion of 7/10 on two consecutive sessions was applied (significantly

240 above chance for a probability of success of 0.33); at the time of making this decision this button had been
241 chosen in 4% of cases from a total of 390 trials with 7 pairs. The reason for the apparent avoidance is unclear as
242 the button furthest from the experimenter was not the most common choice at this point and the avoidance was
243 not as strong by the end of the experiment (see results section below). Pairs or individuals completed a
244 maximum of 18 sessions.

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

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

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

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

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

268 **Analysis.** To test the effect of condition on the number of sessions to successful coordination and the

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

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

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

292

293 **Results and Discussion**

294 Overall, the results show that chimpanzees are able to solve this coordination problem. With their first
295 partner in the dyadic condition most pairs (7/8) could eventually coordinate reliably. This coordination success
296 could be achieved in several different ways. One is by simply returning to a successful button, without any
297 consideration of the behavior of their partner. Alternatively, with an understanding of the role of the partner,

298 coordination could be achieved by responding to, predicting or influencing a partner's choices. To investigate
 299 this, we recombined pairs. If, through experience with the task, they had developed a flexible coordination
 300 strategy based on the decisions of themselves and their partner they should reach criterion more quickly with
 301 subsequent partners. We did not find evidence that pairs became quicker to coordinate with their new partners
 302 ($Mdn=11$ sessions, 95% CI [6, 18]; $\chi^2_4=2.1$, $p=0.71$, $N=23$; see Figure 2(a)). There were also no significant
 303 differences between pairs tested before completing the solo condition and those tested after passing the solo
 304 condition (comparing first partners only: $\chi^2_1=0$, $p=0.95$, $N=8$) nor between groups A and B ($\chi^2_1=0.7$, $p=0.40$,
 305 $N=23$). As a second measure of coordination success we analysed the number of successful trials in the first
 306 session and found no evidence of improvement in first session success across partners ($M=3.0$, $SD=2.7$; $\chi^2=$
 307 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
 308 (see Figure 2a; chance=2.5 trials).

309 The majority of chimpanzees (13/16) passed the solo condition. They were able to solve the task more
 310 quickly alone than in the dyadic condition ($Mdn\ solo=4$; $Mdn\ dyadic=10$; $W=29$, $p<0.01$, $N=11$, Mdn
 311 difference=6.5, 95% CI [2, 10]) but there were no significant differences between conditions in first session
 312 success ($W=16.5$, $p=0.79$, $N=11$, Mdn difference=0.5, 95% CI [-7, 5]). There were also no differences between
 313 groups in the solo condition in either measure (number of sessions: $Mdn\ Group\ a=5.5$, 95% CI [4, NA]; Mdn
 314 $Group\ b=4.0$, 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
 315 difference between conditions indicated that coordinating with a partner created an additional challenge for the
 316 chimpanzees. It should be noted that the increase in sessions to success in dyadic condition is based on
 317 comparison between two separate social groups (housed in the same zoo with auditory and limited visual access
 318 to each other), so it is possible that group differences rather than experimental manipulation underlies this effect.
 319 However, we did not have any a priori expectations for differences in performance between groups and we did
 320 not find any significant differences in our main measures, increasing our confidence that this is a condition
 321 effect. Each of the four possible solutions to the task (i.e. each set of buttons) resulted in an equal value of
 322 reward; thus, if partners were coordinating flexibly with their partner they could potentially coordinate on the
 323 whole range of solutions. However, pairs tended to converge on one single set of buttons ($M=1.21$ sets per
 324 session per pair, $SD=0.22$), presumably by choosing the option that had previously led to success. One possible
 325 explanation for this is that one set of buttons was perceptually salient and thus attracted the attention of both
 326 individuals to it, leading them to choose this preferentially and consequently to coordinate. In contradiction to

327 this explanation, there was no indication of a clearly preferred option overall: there was some evidence of
328 avoidance of the button closest to the experimenter (representing 12% choices) but choices were distributed
329 evenly across the remaining three boxes (representing 28-31% choices each). We used this variation across pairs
330 to reduce the likelihood of pairs coordinating by chance: each new pairing, as far as possible, was made up of
331 individuals who had coordinated on a different set of buttons in the previous round. Thus, in achieving
332 coordination with new partners, chimpanzees did show some flexibility.

333 Individuals in the solo condition also generally used one set of buttons ($M=1.33$ set per session per pair,
334 $SD=0.25$), but the distribution of choices differed to that of the dyadic condition ($\chi^2_3=191.33, p<0.01, N=7086$).
335 The pattern suggests that each pair converges on one set of buttons (and this differed between pairs). This results
336 in successful but somewhat inflexible coordination, as new solutions to the problem need to be re-established
337 with new partners.

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

341

342 **Study 2: Children's coordination**

343

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

348

349 **Materials & Methods**

350 **Subjects**

351 Forty 4 year old children were included in the final analyses; 20 boys and 20 girls ($M_{age}=50.8$ months,
352 range =48-54 months). We chose 4 year olds to provide a comparison to a previous coordination game also
353 played by 4 year old children and chimpanzees (Duguid et al., 2014). Additionally, pilot testing indicated that
354 this was the youngest age that they reliably engaged in the task. They were paired in 47 dyads, with each child

355 tested with up to 3 different partners. Both children in the dyad were from the same kindergarten, but not
356 necessarily the same class (26 dyads from the same class and 21 from different classes). In order to maximise
357 the number of potential dyads children were paired with same and different sex partners (mixed-sex = 29 dyads,
358 female = 9 dyads, and male = 9 dyads). A further 11 children completed the training but were not included in the
359 final sample either because there was no partner available for them (i.e. there was an odd number of children at
360 a particular kindergarten, $N=3$ children), or because they were not available to complete the required number of
361 sessions with their first partner ($N= 8$ children). All testing took place at kindergartens in the Leipzig city area,
362 Germany; the children were recruited from a database of parents who volunteered to take part in child
363 development studies.

364

365 **Materials**

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

375

376 **Procedure and Design**

377 **Training.** The first experimenter introduced herself during a short warm-up phase and engaged the
378 child in conversation before starting the training. A second experimenter operated and reset the apparatuses but
379 most of the interaction was with the first experimenter to reduce the likelihood that children would engage the
380 second experimenter during the task. Children completed the same four training phases as the chimpanzees.
381 They were trained individually and completed all phases in one session in order to reduce the total number of

382 testing days. One additional trial with the single-choice box was added to the end of the children's training so
383 that the session would end with a positive experience.

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

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

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

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

405 All children were tested with up to three partners in the dyadic condition. In contrast to the
406 chimpanzees they were always tested in the solo condition after completing the dyadic condition. As in study 1,
407 pairs that successfully coordinated were re-shuffled. Only children who successfully coordinated with a first
408 partner were paired with a second partner and third partner. In some cases, children were not available, or a
409 partner was not available to be tested with a second or third partner. In total 19 dyads were first partners; 18
410 dyads were second partners; and 10 dyads were third partners. As far as possible, chimpanzees were shuffled in

411 a way that would minimise the likelihood that new partners would coordinate by chance by pairing individuals
 412 that had converged on different buttons with previous partners. This was not possible for child dyads as they did
 413 not show the same pattern of convergence (see section 3.2). As many subjects as possible were tested in the solo
 414 condition, after completing the dyadic condition (N children tested after first partner=4, second partner =11,
 415 third partner =14).

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

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

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

433 **Analysis.** The main analyses were performed as in Study 1 for comparability: non-parametric survival
 434 analysis to test the effects of partner number, gender (girls, boys or mixed pairs), and whether they were in the
 435 same kindergarten class on the number of sessions to successful coordination. GLMM's were used to test the
 436 effects of the same predictors on coordination success in the first session. To compare independent samples of
 437 first session success in the dyadic condition to the solo condition, we compared pairs tested with a third partner
 438 to individuals tested in the solo condition after their second partner using a Wilcoxin rank-sum test. Since all

439 children completed the solo condition only after the dyadic condition this was the best comparison to the
 440 chimpanzees' data that controlled for experience (see ESM for further details).

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

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449 **Results and Discussion**

450 **Children's Coordination**

451 The four year old children were very successful at coordinating in this task. This was already evident
 452 with their first partner. All 19 of the initial pairings reached criterion and did so very quickly ($Mdn=3$ sessions,
 453 95% CI [2, 3]). The picture was similar with second and third partners (see Figure 2(b)). With their second
 454 partner most pairs reached criterion (16 of 18), and in a median of 2 sessions (the minimum possible, 95% CI [2,
 455 4]). With their third partner all pairs were successful (10/10; $Mdn = 2$ sessions, 95% CI [2, NA]). Overall, the
 456 number of sessions required to coordination reliably did not decrease significantly with the number of partners,
 457 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
 458 reaching the criterion so quickly from the onset. There was significant improvement in first session success
 459 across partners (estimate \pm s.e.= 0.24 \pm 0.10; $\chi^2= 5.26, df= 1, p=0.02, N=47$, see Figure 2(b)). There were no
 460 significant effects of the sex of the dyad or whether they were from the same kindergarten class on either
 461 measure of performance.

462 Pairs of children were coordinating on a wide range of solutions within each session: about two-thirds
 463 of pairs were using three or four sets of buttons within a session ($M=1.94$ buttons used per session per dyad,
 464 $SD=0.94$). As there were only five trials per session, this meant that for many pairs their coordination was
 465 flexible enough to switch between buttons on almost every trial. However, a significant number of pairs were
 466 also very similar to the chimpanzees: converging on one or two buttons.

467 Children were also very successful in the solo condition. Due to time constraints the solo condition
 468 was restricted to two sessions, and they either passed immediately ($>4/5$ on both sessions) or failed. The
 469 majority of children passed within these two sessions (24 of 29). A comparison of performance in the first
 470 session between solo and dyadic conditions shows no significant difference ($W=57, p=0.90, N=21, Mdn$
 471 $difference < 0.01, 95\% CI [-1, 1]$). This suggests that coordinating with a partner was no more difficult than
 472 completing the task independently.

473

474 **Comparison of coordination between children and chimpanzees**

475 A more detailed analysis of successful coordination in both species suggests two ways in which
 476 children's coordination differed from the chimpanzees. We compared the behaviour of the chimpanzees in Study
 477 1 to the children in Study 2. The relative timing of decisions indicates the first way in which coordination
 478 differed, in this context. One way to solve this coordination problem is a leader-follower strategy: one partner
 479 waits for the other to act first and then follows her lead. This is particularly efficient in situations with complete
 480 visual access and abundant time to make decisions such as the current task. We compared the proportion of
 481 decisions that were made simultaneously (within 1s of each other) with those that were sequential ($>1s$ between
 482 decisions), with the assumption that increased time between decisions allows for the possibility of a leader-
 483 follower strategy. In the majority of trials children made sequential decisions, more so than chimpanzees
 484 ($M_{children}=72.85\%$ sequential decisions per dyad, $SD= 22.93$; $M_{chimpanzees}=43.99\%$, $SE=27.70$; $estimate \pm s.e. =$
 485 1.50 ± 0.44 ; $\chi^2= 10.36, df= 1, p < 0.01, N=1227$ trials). This is consistent with the idea that children were following
 486 a partner's decision. It would also explain how some children ($N=5$) did not perform above chance in the solo
 487 condition but were successful in the dyadic condition: as long as one individual can wait for their partner to
 488 initiate, they can follow.

489 A second way to coordinate is to communicate decisions to a partner. Children were more likely to
 490 communicate to each other about the task (via gestures or vocalisation) than chimpanzees were
 491 ($M_{children}=26.22\%$ trials per dyad, $SD= 33.46$; $M_{chimpanzees}=3.12\%$, $SD=5.10$; $estimate \pm s.e. = 2.69 \pm 0.90$; $\chi^2= 8.01,$
 492 $df= 1, p < 0.01, N=1227$ trials). In most cases this included a verbal and/or gestural reference to a specific choice,
 493 e.g. saying "here" while pointing to the button they had/were about to choose (78.10% trials with
 494 communication included an act of reference to a specific choice), rather than more general attention-getters such
 495 as calling their partner's name. Children often communicated before either of them had made their decision

496 (54.01% trials with communication were pre-decision). This is different from the type of communication
497 observed with the chimpanzees: in the few instances in which they did communicate they used gestural
498 attention-getters, but did not refer to specific choices. Typically, this involved a noisy gesture towards a partner
499 (e.g. knocking in the wire mesh between the cages) while waiting for them to make their decision after having
500 already made their own choice. We reduced the likelihood of coding signs of general frustration with the task by
501 coding gestures directed towards the partner, however, to better determine whether the behaviours we observed
502 were intended to solicit action from the partner, we would need an additional version of the task in which
503 communication was not possible.

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

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General Discussion

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

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523 Our results extend previous findings showing that four year old children are able to cooperate and
524 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

525 interactive context where they are able to see each other and communicate freely. This ability makes way for the
526 capacity to coordinate with absent partners (when no communication is possible) at the age of 5 or 6 using skills
527 such as second-order theory of mind or cultural common ground (Goldvicht-Bacon & Diesendruck, 2016;
528 Grueneisen et al., 2015a; Grueneisen et al., 2015b).

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

547 The overall pattern of coordination was qualitatively different for the chimpanzees: as well as taking
548 several sessions to reach criterion they did not quickly adapt to new partners, converging to a single set of
549 buttons rather than flexibly switching between them. One explanation for this pattern is that individuals simply
550 return to successful buttons without any consideration of their partner's actions. This explains the time required
551 to establish reliable coordination, but it is efficient once achieved. It is not possible to rule out this strategy,
552 however, two findings suggest that this does not completely account for their decisions. The first is that
553 individuals were quicker to solve the task alone than with a partner, indicating that coordinating with a partner is
554 an additional challenge but one that many of them did eventually succeed in. Secondly, chimpanzees did

555 communicate with attention-getters to engage a partner while waiting for their partners to choose, indicating an
556 understanding that the partner's action is necessary. This form of communication is similar to the way
557 chimpanzees have communicated in previous experimental situations in which they required help from
558 conspecifics e.g. (Yamamoto, Humle, & Tanaka, 2012; Yamamoto & Tanaka, 2009). Our evidence suggests that,
559 chimpanzees in this task do take into account that a partner needs to act but not which actions a partner takes
560 within a test trial. Once pairs discover a successful solution, they can maintain success with the same partner
561 without communicating or even monitoring their decisions.

562 Previously, Bullinger et al. (2011) suggested that chimpanzees were using a leader-follower strategy, to
563 coordinate their decisions in a stag hunt coordination problem. This strategy could account for the condition
564 differences in the present coordination problem: when operating the puzzle-box alone, their actions were always
565 sequential so the information about their own choice was always available. However, in the dyadic condition
566 this did not appear be the main strategy, individuals did not wait for information about their partner's choice. In
567 other cooperative tasks chimpanzees have shown that they are capable of waiting in order to work together (e.g.
568 the 'loose string' task; (Hirata & Fuwa, 2007; Melis et al., 2006; Melis, Hare, & Tomasello, 2009). These
569 studies, however, have included training during which individuals learn that any action before the arrival of a
570 partner results in task failure. In the current set up, waiting only provides useful information about a partner's
571 decision but is not necessary to operate the puzzle box successfully. Although apes have been shown to inhibit
572 choices to seek information actively in non-social contexts (e.g. Bohn, Allritz, Call, & Völter, 2017; Call, 2010),
573 evidence from cooperative tasks suggests that this may be more difficult in social contexts (Bullinger, Melis, &
574 Tomasello, 2014 and the current study). Further studies would be necessary to determine whether factors such as
575 task complexity, inhibition or metacognitive skills contribute to this apparent difficulty. Another difference
576 between the current task and that of tasks like Bullinger et al. (2011), and more recently Melis & Tomasello
577 (2019), that would make a leader follower strategy more challenging is that the dimensions of the apparatus
578 preclude the use of body position of the partner to indicate a choice. Instead the chimpanzees have to focus on
579 manual actions or gestures, or the apparatus itself, which may be less salient signals.

580 Investigating the proximate mechanisms of human and chimpanzee collaboration in a mutualistic
581 context is key to fully understanding the evolution of human cooperation (Balliet, Tybur, & Lange; Balliet et al.,
582 2017; Tomasello, 2016) and our results contribute to the developing picture of the way chimpanzees and
583 children coordinate their decisions. In previous experiments where the costs of coordination failure were low
584 and there was a salient, high value choice both chimpanzees and children were very successful at coordinating

585 their actions with a partner (Hirata & Fuwa, 2007; Melis et al., 2006; Melis et al., 2009; Wyman et al., 2013).
586 However, when the costs increase (Duguid et al., 2014) and when efficient coordination requires coordination of
587 decisions (such as in the current task) humans seem to excel. The way in which communication is used by both
588 species indicates significant differences in their coordination strategies: children are engaging with their peers to
589 solve the problem together even before making any choices, while chimpanzees seem to solve the problem more
590 individualistically. The current task was designed specifically to investigate coordination when it is difficult to
591 make predictions about a partner's behaviour (because all the options are of equal value and effort). However, to
592 understand how chimpanzees coordinate decisions during activities such as group hunting or decisions about
593 travel directions, another essential avenue of research will be to examine whether chimpanzees use the same
594 socio-cognitive abilities shown in competitive tasks to predict conspecific behaviour in cooperative contexts and
595 coordinate with them (e.g. Grueneisen, Duguid, Saur, & Tomasello, 2017; Karg, Schmelz, Call, & Tomasello,
596 2015). If these abilities are context-specific we can gain a clearer picture of the of proximate mechanisms
597 underlying coordination in chimpanzees as well the evolutionary history of human cooperation. Overall, the
598 current results are consistent with the view that humans have evolved socio-cognitive skills supporting the
599 ability to coordinate decisions effectively in the context of mutualistic collaboration.

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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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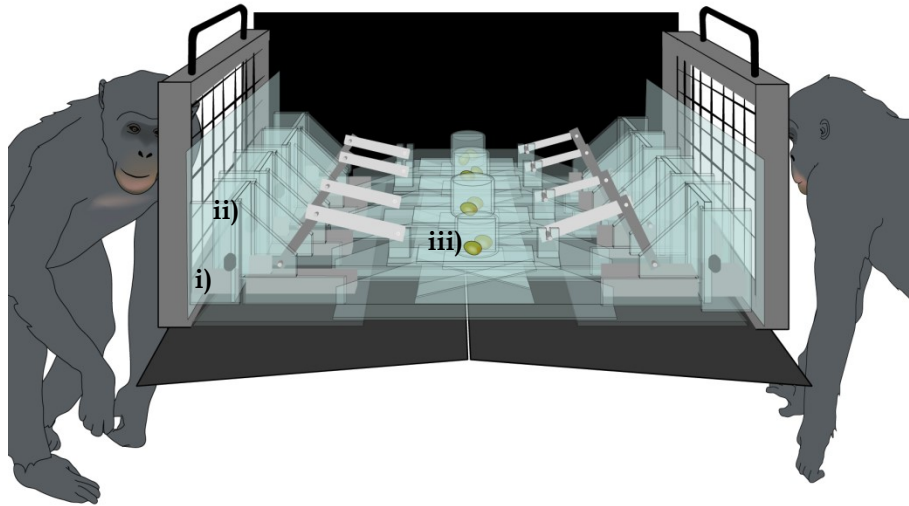
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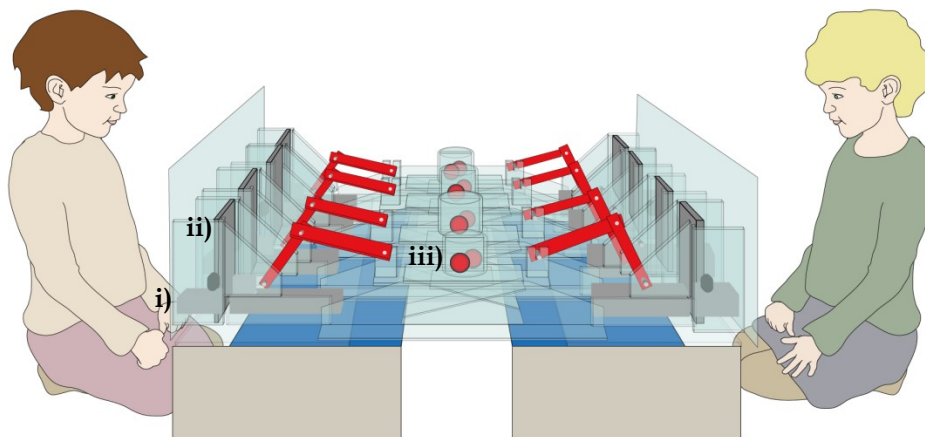
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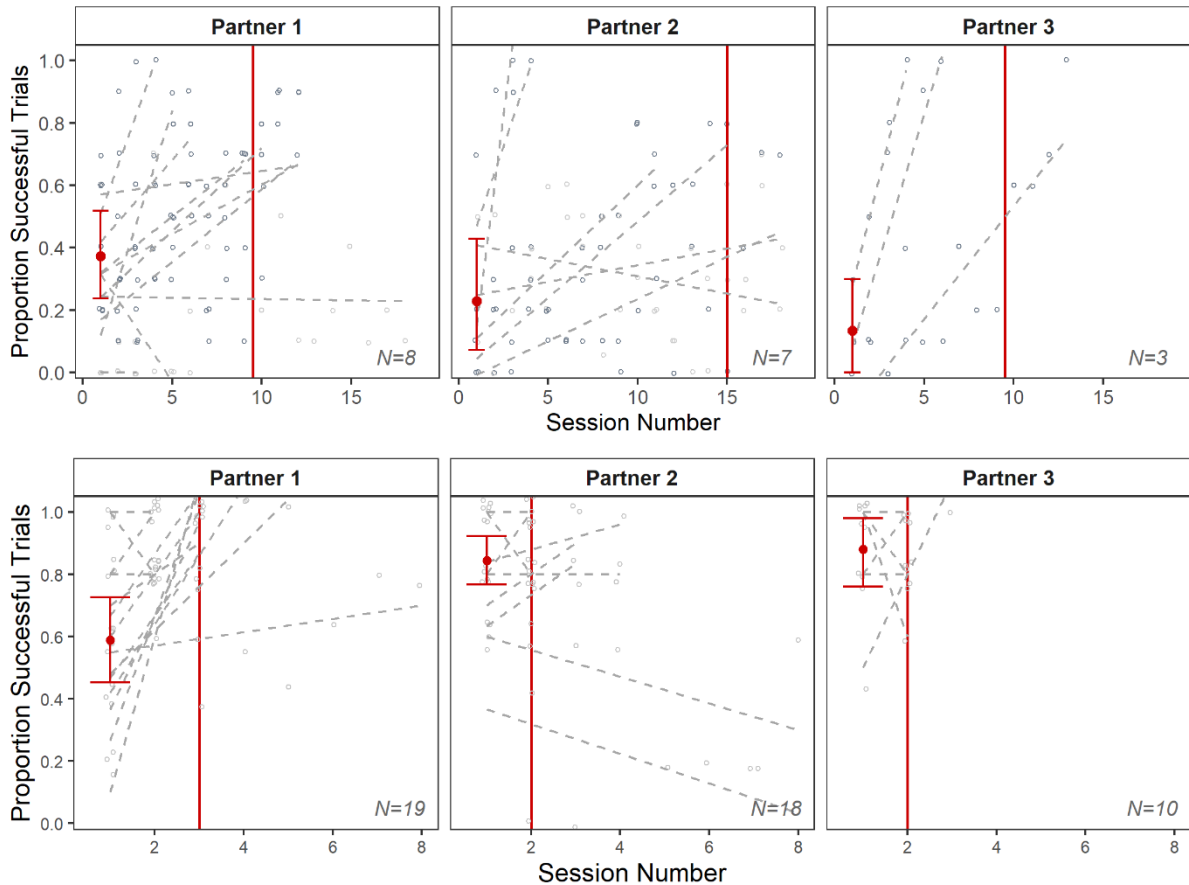
743 b)



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745

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



750

751 *Figure 2.* Coordination success across sessions for chimpanzees (a) and children (b) for partner numbers 1-3.

752 The red vertical line indicates the median number of sessions to reach criterion. The red point (+ 95% CI)

753 indicates the mean success in session 1. Each pair tested is represented by a dashed line.

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