

Est.
1841

YORK
ST JOHN
UNIVERSITY

Duguid, Shona, Sánchez-Amaro, Alejandro, Call, Josep and Tomasello, Michael (2016) Chimpanzees coordinate in a snowdrift game. *Animal Behaviour*, 116. pp. 61-74.

Downloaded from: <https://ray.yorks.ac.uk/id/eprint/9191/>

The version presented here may differ from the published version or version of record. If you intend to cite from the work you are advised to consult the publisher's version:

<https://www.sciencedirect.com/science/article/abs/pii/S0003347216300045>

Research at York St John (RaY) is an institutional repository. It supports the principles of open access by making the research outputs of the University available in digital form. Copyright of the items stored in RaY reside with the authors and/or other copyright owners. Users may access full text items free of charge, and may download a copy for private study or non-commercial research. For further reuse terms, see licence terms governing individual outputs. [Institutional Repositories Policy Statement](#)

RaY

Research at the University of York St John

For more information please contact RaY at
ray@yorks.ac.uk

1 TITLE: Chimpanzees coordinate in a Snowdrift Game.

2 AUTHORS: Alejandro Sánchez-Amaro¹, Shona Duguid¹, Josep Call^{1,2} & Michael Tomasello¹

3

4

5

6 AFFILIATION:

7 ¹ Max Planck Institute for Evolutionary Anthropology, Developmental and Comparative Psychology,

8 Leipzig, Germany.

9 ²School of Psychology and Neuroscience, University of St. Andrews, Scotland, United Kingdom.

10

11

12

13

14

15

16

17 First author correspondence: Alejandro Sánchez-Amaro, alex_sanchez@eva.mpg.de, +49 341 3550 423,

18 Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary

19 Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany.

20

21 **Abstract**

22 The snowdrift game is a model for studying social coordination in the context of competing interests.
23 We presented pairs of chimpanzees with a situation in which they could either pull a weighted tray
24 together or pull alone to obtain food. Ultimately chimpanzees should coordinate their actions because
25 if no one pulled, they would both lose the reward. There were two experimental manipulations: the
26 tray's weight (low or high weight condition) and the time to solve the dilemma before the rewards
27 became inaccessible (40 seconds or 10 seconds). When the costs were high (i.e high weight condition),
28 chimpanzees waited longer to act. Cooperation tended to increase in frequency across sessions. The
29 pulling effort invested in the task also became more skewed between subjects. The subjects also
30 adjusted their behaviour by changing their pulling effort for different partners. These results
31 demonstrate that chimpanzees can coordinate their actions in situations where there is a conflict of
32 interest.

33 **Keywords:** chimpanzees, conflict, cooperation, coordination, decision-making, snowdrift game.

34

35

36 Social species need to coordinate with others to benefit from living in a group. However, in many cases
37 individuals have competing interests. For instance, chimpanzees (Boesch, 1994, 2002) and lions (Scheel
38 & Packer, 1991) are more successful when they hunt and defend their territories as a group; but
39 individuals may be tempted to lag behind to avoid potential costs (e.g., risk of injury) and benefit from
40 others' efforts (Gilby & Connor, 2010).

41 Previous experimental studies have found that when individuals need to work together to retrieve food
42 chimpanzees can coordinate their actions (Chalmeau, 1994; Cronin, Bridget, van Leeuwen, Mundry &
43 Haun, 2013 Hirata & Fuwa, 2007; Melis, Hare & Tomasello, 2006; Suchak, Eppley, Campbell & de Waal,
44 2014). To a certain extent, chimpanzees can also coordinate their actions when there is an alternative
45 (though lower-value) reward that can be obtained individually (Duguid, Wyman, Bullinger, Herfurth-
46 Majstorovic & Tomasello, 2014). Even when Melis, Hare and Tomasello (2009) introduced a conflict of
47 interest by presenting chimpanzee pairs with a choice between two cooperative tasks, one with equal
48 payoffs (3-3) and other with unequal payoffs (5-1), pairs still cooperated in the majority of trials. In
49 contrast, Bullinger, Melis and Tomasello (2011) found that chimpanzees preferred to work alone to
50 obtain the same amount of food. Their preference for solitary over social work, however, was reversed
51 when the payoff of the social option was higher than the payoff of the solitary option. The subject's
52 preference for the non-social option suggests that they did not take into account their partner's
53 preference because the partner could not obtain the rewards by pulling alone.

54 In previous studies that did not offer subjects an alternative non-social option (but see Bullinger et al.,
55 2011), subjects needed to cooperate with a partner to complete the task regardless of the payoff's
56 distribution (Melis et al., 2009) or time constraints (Duguid et al., 2014). However, in some situations
57 such as group hunting, initiating the action and investing energy in a cooperative act is not necessarily
58 the best strategy from an individual's perspective as it is a costly and risky action (Gilby & Connor, 2010).

59 Therefore, if a group member starts a hunt, others can benefit without actively participating and
60 incurring the costs. However, if no one starts the hunt, they all lose the chance to get the prey. How can
61 chimpanzees solve this dilemma? According to Boesch (2002), chimpanzees coordinate to take specific
62 roles when initiating a hunt, providing a cooperative solution to the dilemma. However, chimpanzees
63 may use other strategies when initiating the hunts. For instance Boesch (2002) reported that young
64 chimpanzees tended to start the chase. This could be explained if we consider that young chimpanzees
65 did not fully understand the contingencies of the hunting endeavour and therefore were willing to
66 initiate it whereas more experienced chimpanzees lagged behind (see Tomasello, 2009). Similarly, a
67 study by Gilby et al. (2015) found evidence that some chimpanzees, described as “impact-hunters”, are
68 willing to pay the extra costs to begin the hunt, letting others join in when the risks are lower. The
69 dilemma faced by individuals in such situations is thus whether to initiate the action or not, given that if
70 no-one initiates everyone loses out. In theory, each individual’s preference ranking should be that: (1)
71 other begins, (2) I begin, (3) no one begins. Despite the observational work of previous studies (Boesch,
72 2002; Gilby et al., 2015) there has been little experimental work studying how chimpanzees would
73 behave in situations where a conflict of interest is present (but see Schneider, Melis & Tomasello,
74 2012).

75 These types of interactions have been modelled by theorists in the snowdrift game (Doebeli & Hauer,
76 2005; Kun, Boza & Scheuring, 2006; Sudgen, 1986). In the classic description of the snowdrift situation
77 two cars become stranded on a highway that is covered with snow. The snow must be shovelled off the
78 road before the drivers can return home. They could shovel the snow together and share the work, or
79 alternatively, one driver could do it alone. Each driver would prefer that the other one do it. However, if
80 one of them defects the other should shovel the snow, thus paying the costs to return home. So in the
81 snowdrift dilemma, subjects have a common goal that can be either achieved by performing a
82 cooperative act (either together or individually) or free-riding. Of course, it is in the interest of each

83 subject to defect and let the partner incur the cost but if neither pays the costs both lose. According to
84 recent literature (Kun et al., 2006) chimpanzee hunting could be explained by applying the metaphor of
85 the snowdrift game. Chimpanzees would prefer others to start the hunt unless no one else starts. In the
86 latter case, as in the previous example, the chimpanzee would prefer to begin the hunt rather than let
87 the monkey escape. So, unlike in the prisoner's dilemma (Axelrod & Hamilton, 1981; Maynard-Smith,
88 1982) acting cooperatively can avoid the worst-case scenario as a cooperative act will always provide a
89 benefit, even for the subject that carries out the costly action.

90 Besides agent-based model studies, the snowdrift game has been empirically applied to study human
91 strategic behaviour (Duffy & Feltovich, 2002; 2006; Kümmerli et al., 2007; Rapoport & Chammah, 1966).
92 Overall, these studies have found that humans cooperate more when they are faced with a snowdrift
93 game in comparison to the prisoner's dilemma situation. However, as far as we know the snowdrift has
94 not yet been used to study strategic decision-making in non-human primates.

95 The aim of this study was to use the snowdrift model to investigate how chimpanzees solve a
96 coordination task with a conflict of interest. We presented pairs of chimpanzees with a version of the
97 snowdrift game in which they obtained food rewards by pulling a weighted tray towards them. They
98 could either perform a cooperative act (pull the rope and do all the work or both pull and thus share the
99 load) or one could free-ride while the other did the work. Importantly, chimpanzees were free to decide
100 the amount of weight they pulled. Therefore, cooperation, defined by both individuals pulling during the
101 same trial, could be skewed towards one subject depending on the efforts invested by each member of
102 the dyad. In real-life situations, chimpanzees are able to vary their degree of investment by starting the
103 chase, follow other individuals and join the chase or lag behind and reap the benefits from the hunt
104 (Boesch, 2002; Gilby et al., 2015). For instance, in the case of hunting, chimpanzees could theoretically
105 initiate the hunt but then let others do most of the work, although to our knowledge this has not been

106 empirically demonstrated. Therefore subjects are not only faced with a binomial decision (either
107 cooperate or free-ride) as in previous cooperative games (Chalmeau, 1994; Duguid et al., 2014 Hirata &
108 Fuwa, 2007; Melis et al., 2006, 2009) but can adjust their actions by investing different amounts of effort
109 (i.e. their speediness in chasing the monkey), allowing them to make precise decisions based on the
110 physical contingencies and the partners' actions. In our task both subjects got the same amount of food
111 as long as one individual pulled, so there was no need for cooperation. However, if neither pulled within
112 a certain time-frame both lost the food. This set up reflects the payoffs of the 2-person snowdrift game
113 where the best strategy for a chimpanzee was to wait for the partner to pull and obtain the benefit (b)
114 but pay the cost of the action if the partner did not pull ($b-c$) to avoid losing the rewards if no one pulls
115 ($b = 0$). At the same time, if both partners pull simultaneously, that results in an intermediate
116 cooperative strategy where costs are divided ($b-c/2$).

117 Importantly, although this set-up uses the same payoff matrix as behavioural economic experiments
118 with adults, it differs from these studies in that chimpanzees in our task were not strangers and they
119 were free to interact during the task. However, this set-up is more ecologically valid for chimpanzees
120 because interactions with strangers are relatively rare and often aggressive; cooperation occurs
121 between known group members (Boesch et al., 2008).

122 Our main interests were whether chimpanzees a) would maximize their benefit (food – cost of pulling)
123 by waiting for a partner to pull first, b) would solve the task (get the food) by cooperating or free-riding,
124 c) change their strategies with different partners. We manipulated weight and time to approximate the
125 contingencies of chimpanzee hunting: the apes have to overcome the costs to initiate the action (the
126 weight that they have to move) while the prey is only available for a limited time (the time limits). If
127 chimpanzees acted strategically, we expected them to wait longer to pull when the costs of pulling the
128 tray were high (i.e. it was heavy) and for one individual to free-ride more often (understood as not

129 pulling at all) while the other always pulled. In contrast, during low weight trials we expected
130 chimpanzees to pay less attention to their partners' actions and thus wait less to pull. We also expected
131 chimpanzees to wait longer in long time trials as they would have more opportunity to free-ride
132 compared to short time trials. Our study consisted of two phases: all subjects completed the test with
133 one partner first before partners were re-shuffled for a second round. With this manipulation we could
134 study the overall effect of experience and whether they were able to adjust their actions to the
135 behaviour of their partners as they should not only consider the physical contingencies of the task
136 (weight and time) but also their partners' decisions to maximize their rewards and coordinate their
137 actions.

138 **MATERIALS AND METHODS**

139 *Subjects*

140 We tested 7 female and 5 male captive chimpanzees, *Pan troglodytes* ($X_{age}=23.4 \pm 13.8$, range 9-39 years)
141 housed at the Wolfgang Köhler Primate Research Center in Leipzig Zoo, Germany. In phase 1 of the
142 study all 12 made up 6 unique pairings. In phase 2 10 of the 12 made up 5 new pairings. The
143 experimental set-up required subjects to be in the same cage during testing. Consequently, we could
144 only pair chimpanzees with a high degree of tolerance. Additionally, we paired them according to similar
145 weight (as a proxy for strength).

146 The task required subjects to obtain out-of-reach food rewards (one 4cm banana piece for each
147 individual) by pulling on ropes to move a tray towards them (Fig. 1). Each subject had access to one of
148 two ropes and the tray could be pulled with either one or both ropes. The weight of the tray (and thus
149 the effort required to pull it in) could be adjusted by the experimenter. The weight (in kg) pulled by each
150 individual was measured by two sets of scales that connected each of the ropes to the central weight.
151 We recorded all measurements displayed on each of the scales for the duration of the trial with a digital

152 camera and averaged them for each individual per trial (see Appendix for further methodological
153 details).

154 A 1.09 meter mesh barrier split the tray into two equal parts ensuring that each subject could only
155 access one rope and one side of the tray (with its corresponding food). There were approximately
156 another 1.5 meters between the end of the mesh barrier and the room's back wall. This means that
157 subjects could still move around the room but they were unable to grab both their own and their
158 partner's rope / food simultaneously. To reduce the likelihood that subjects would move around the
159 barrier to steal from one another, trials were started when each chimpanzee was positioned in front of
160 the apparatus on opposite sides of the mesh barrier (Fig. 1).

161 The food rewards were placed in small bowls on either side of the apparatus and the bowls could be
162 moved towards the edge of the tray by the experimenter pulling a nearly invisible piece of fishing line.
163 Once the bowls reached the edge of the tray they fell, together with the food rewards, and became
164 inaccessible (see Appendix for further methodological details).

165

166 The training consisted of two parts. At first, each chimpanzee had to perform an individual training
167 session to understand the physical contingencies of the apparatus. On the next testing day, pairs of
168 chimpanzees that previously succeeded in the individual training performed a dyadic training session to
169 understand and experience all three possible outcomes during the following test phase (see below).
170 During both training sessions (individual and dyadic) only low weight was used to keep subjects
171 motivated during the training sessions. However, experience with high weight was provided prior to
172 starting with high weight sessions.

173

174 *Individual training*

175 Each subject had to perform an individual training session composed of 8 trials: four long time trials
176 where the food remained on a tray for 40 seconds (30 seconds in a static position on the tray + 10
177 seconds moving towards the edges of the tray) and four short time trials where the food remained for
178 10 seconds (constantly moving towards the edges of the tray from the beginning of the trial). These two
179 time conditions were the same across all training and test sessions. Subjects had to pull 8 times to
180 receive the rewards (both sides of the apparatus were baited). Each subject pulled four times (2 times
181 per condition) from the right side of the apparatus and four from the left side. All conditions were
182 randomised within the session (also during dyadic training and the test sessions).

183 *Dyadic training*

184 Each dyad completed one training session together. The session was composed of 12 trials: in four trials
185 both subjects had access to their own rope; in the remaining 8 trials only one subject had access (4 trials
186 for each). We are aware that during this training session, chimpanzees experienced more trials where
187 they had to pull compared to trials where they did not pull. However, we wanted chimpanzees to
188 experience the three potential outcomes that they could face during the test sessions (pull alone, pull
189 together and not pull). Each training condition included two short trials where the food remained for 10
190 seconds and two long trials where the food remained for 40 seconds. In this training each subject
191 experienced four trials pulling together with the partner, four pulling alone to obtain the reward and
192 four not pulling but getting a reward. We could not control the pulling side as in the individual training
193 because the chimpanzees were free to move between sides although we controlled the amount of trials
194 per condition that each chimpanzee pulled by waiting until both chimpanzees were positioned in front
195 of the apparatus.

196

197 *Test sessions*

198 Each dyad performed eight test sessions: four heavy weight sessions (mean weight of tray = 70.64 kg)
199 and four light weight sessions ($X = 26.96$ kg). Each session consisted of 8 trials: four long trials, in which
200 the food rewards were available for 40 seconds and four short trials in which the food was available for
201 10 seconds before falling off the tray. Chimpanzees could differentiate conditions once the trial started.
202 In long trials the food was stationary until the last 10 seconds when it moved towards the end of the
203 tray. In short trials the food started to move when the trial started. As the subjects were free to move
204 between the sides of the apparatus, we could not counterbalance their positions at the beginning of
205 each trial.

206 Prior to each test session subjects were given two individual trials to experience the weight they were
207 going to face in the subsequent session (on the same day). These trials served to inform the subjects
208 about the weight they would face in the following test session and to be sure they could move the
209 weight alone. Although it was not possible to visually detect weight differences in the apparatus, we
210 expected subjects to rely on the information provided in these two trials to make decisions in the test
211 trials. These trials were the same as in the individual training.

212 *Coding*

213 We measured the outcome of chimpanzees' actions (success/failure), the weight each partner pulled,
214 and the timing of pulling. To evaluate all possible instances of cooperation we calculated a "measure of
215 equality" (ME) based on the weight pulled by both subjects on a given trial. To measure the ME we
216 calculated the average of the weights (higher than 1.5 kg) shown on the scales while the subjects were
217 pulling from their ropes. We then divided the difference between averages of the two subjects by the
218 sum of both averages. Therefore, we obtained a "measure of equality" (ME), ranging from -1 to 1. We
219 transformed all of the values to positive values for analysis. Thus, an ME of 1 indicated perfect

220 cooperation (subjects pulled an equal weight) while 0 indicated complete free-riding (only one individual
221 pulled; see Appendix for further details). Importantly, by using this measure, we could identify the exact
222 degree of cooperation (the investment by each subject). To assess whether subjects waited for a
223 partner to pull we recorded the time between the start of the trial and the first subject of the dyad to
224 pull. This was possible as we recorded all sessions with digital cameras and we could calculate times up
225 to 1/25 of a second (see Appendix for further details). We analysed whether the subjects that were
226 tested in two pairs ($N=10$) changed their behaviour (based on the weight moved) with different
227 partners. The inter-observer agreement was excellent based on the 15% of the data ($R^2 = 0.99$) and
228 latencies ($R^2 = 0.94$).

229 In a *post-hoc* analysis we investigated whether the partners' previous actions had an effect on the
230 subject's likelihood to pull on a subsequent trial. To do so, we constructed a predictor based on the
231 number of trials in which the subject's partner had pulled within a particular session, prior to the
232 subject's action in a given trial. For example, on trial 8 of the session the partner could have pulled from
233 0 to 7 times. Importantly, we did not take into account the first trial of each session as there was no
234 previous experience.

235 *Ethical note*

236 The study was ethically approved by an internal committee at the Max Planck Institute for Evolutionary
237 Anthropology. Animal husbandry and research comply with the "EAZA Minimum Standards for the
238 Accommodation and Care of Animals in Zoos and Aquaria", the "WAZA Ethical Guidelines for the
239 Conduct of Research on Animals by Zoos and Aquariums" and the "Guidelines for the Treatment of
240 Animals in Behavioural Research and Teaching" of the Association for the Study of Animal Behaviour.

241

242 RESULTS

243 Overall, chimpanzee pairs coordinated their actions and obtained the food in 96.7% of trials.

244 Chimpanzees showed evidence of minimising their costs. In high weight sessions, chimpanzees waited
245 longer to pull across trials while they decreased their latency to pull across trials in low weight sessions
246 (Model 1; LMM: $\chi^2_1 = 6.127$, $N = 586$, $P = 0.013$, $CI [-0.195, -0.022]$; Fig. 2a). Rather than being strategic
247 this finding could be a result of subjects getting tired in later trials. However, they did not show this
248 latency difference between high and low weight trials during the experience trials prior to the test when
249 there was no partner present (Model 2; LMM: $\chi^2_2 = 1.265$, $N = 166$, $P = 0.26$). Moreover, when we
250 analysed the total time that chimpanzees spent pulling, they decreased their time during the last trials
251 of high weight sessions (Model 3; LMM: $\chi^2_1 = 10.76$, $N = 586$, $P = 0.001$, $CI [-0.103, -0.021]$; Fig. 2b) further
252 suggesting that waiting was strategic and not a consequence of fatigue.

253 However, despite indications of strategic behaviour, we found that pulling together (i.e. a $ME > 0$) was
254 the dominant strategy to solve the task: 60% trials in low weight and 79% in high weight. We found that
255 pulling together tended to increase across high weight sessions although the result was not significant,
256 (Model 4; GLMM: $\chi^2_1 = 3.518$, $N = 702$, $P = 0.06$, $CI [-1.911, -0.108]$; Fig. 2c), which suggests that dyads
257 tended to cooperate more often when the effort was high. We report and plot this result as it is an
258 interesting trend in the opposite direction we predicted, suggesting that chimpanzees cooperated more
259 often in high weight trials.

260 While pulling together was common, the effort invested by individuals was often unequal ($X_{ME} = 0.58$)
261 with no significant effects of weight condition on session, trial or type of trials (Model 5; LMM: $\chi^2_8 =$
262 9.716 , $N = 490$, $P = 0.286$). However, the percentage of weight pulled by the first puller increased across
263 sessions in the high weight condition (Model 6; LMM: $\chi^2_1 = 7.252$, $N = 478$, $P = 0.007$, $CI [-0.103, -0.021]$;

264 Fig. 2d) and the percentage of the total weight pulled by the first puller was always greater than 50%.
265 This indicates that being the first to act is more costly, and this cost differential increases with
266 experience.

267

268 Interestingly, the length of the trial neither influenced the timing of their decisions nor their likelihood
269 to cooperate, suggesting that it was mainly the effort and not the time pressure that influenced the
270 subject's actions. Phase (1 or 2) did not have a systematic effect in any of our models, suggesting that
271 previous experience with another subject did not influence the subjects' performance with another
272 partner. However, subjects did change their behaviour between phases: they significantly varied in their
273 effort (46% of difference in weight moved) between partners (Model 7; LMM: $X=45.89$, CI [27.84,
274 63.56]) suggesting that chimpanzees did not act in the same way when they were paired with different
275 partners. Figure 3 shows that the pulling latencies of the subjects overlap suggesting that individual
276 differences in pulling latency do not fully explain the differences observed in pulling effort between
277 subjects (see Appendix for details).

278 Our *post-hoc* analysis on the pulling probability as a function of the previous proportion of partner pulls
279 within a session revealed no significant effect (Model 8; GLMM: $\chi^2_8 = 6.202$, $N = 1228$, $P = 0.4$) neither in
280 high nor in low weight conditions, suggesting that chimpanzees did not take into account their partners'
281 previous decisions to pull when deciding whether to pull or not in a subsequent trial.

282 **DISCUSSION**

283 In a task where chimpanzees could potentially free-ride and benefit from their partner's actions, dyads
284 solved the coordination problem by pulling together, with a tendency to pull more often together when
285 those costs were high. However, there were also indications that chimpanzees acted strategically to

286 minimize their effort: they were more likely to wait longer to pull at the end of high weight sessions and
287 the effort invested by first and second puller was imbalanced. Therefore, although chimpanzees did not
288 free-ride (by not pulling at all) more in high weight conditions as we predicted, they did it so in more
289 subtle ways, by investing unequal efforts. Chimpanzees also differed significantly in the effort they
290 invested when tested with different partners.

291 Previous studies established that chimpanzees cooperate when it is either the only option to get food
292 (Hirata & Fuwa, 2007; Melis et al., 2009) or the option that produces the largest food payoff (Duguid et
293 al., 2014; Bullinger et al., 2011). Here we have shown that chimpanzees cooperate even when there is
294 the option to free-ride. One possible explanation for this outcome is that they do not know that they
295 could free-ride and get the food without pulling because they were trained to pull individually. This
296 means that when they were paired with a partner, they continued to pull as they had done in the past.
297 However, all subjects had experienced that food could be obtained without pulling during the dyadic
298 training. Recall that these subjects experienced receiving food after a partner pulled and they just
299 waited. Moreover, they also experienced pulling and a partner benefiting from the food without them
300 pulling at all. However, to train subjects equally on all outcomes, they experienced more trials where it
301 was necessary to pull compared to trials where they obtained the food without pulling. Thus, it is
302 possible that this effect could have influenced their likelihood to pull.

303 Alternatively, it could be that some chimpanzees were just pulling to obtain the food regardless of the
304 effort and the partners' presence. But if this were true we would not expect to find differences in their
305 latency to pull between conditions. On the contrary, subjects behaved strategically when pulling high
306 weights. Moreover, we would not expect that cooperation tended to increase across sessions when
307 subjects had already experienced in the dyadic training that they could obtain food without pulling, but

308 it increased over time in that condition suggesting that subjects cooperated depending on the effort
309 they were required to contribute and their prior experience.

310 The chimpanzees showed further evidence of minimising their costs: they waited longer for their
311 partner to pull during high weight sessions in which the difference in weight moved between first and
312 second puller increased across sessions. Increased waiting and high levels of cooperation could be a
313 result of subjects trying to avoid being the first to pull because a) initiating the movement of the tray
314 required more pulling effort and b) by pulling second there was no risk of their partner free-riding. As
315 has been already discussed, fatigue seemed not to affect their responses. Therefore subjects were not
316 simply cooperating to share the effort but acted to obtain the rewards and avoid the costs.

317 A more plausible explanation for the high levels of cooperation observed here could be related to the
318 amount of experience with the task; subjects learned that by pulling simultaneously the task became
319 easier and therefore, they continued to pull simultaneously until the end of the study. This would have
320 been especially salient during the high weight condition in which cooperation tended to increase across
321 sessions. The perception of weight reduction driven by its division should have been the same in both
322 conditions (the same proportion between the total weight and the divided weight). However, due to the
323 fact that low weight trials were already easier to perform for all individuals, it is possible that the
324 division of weight in high weight trials would have been more salient for the chimpanzees. Additionally,
325 social facilitation could have contributed to maintain a high level of cooperation. Seeing another
326 chimpanzee pulling led them to pull thus making free-riding less likely (Galloway, Addessi, Frigaszy &
327 Visalberghi, 2005). Finally, it is also possible that the high rate of cooperation that we found were due to
328 the high degree of tolerance between the members of the dyads selected for the study (Hare et al.,
329 2007). This suggestion needs to be corroborated by further studies testing dyads that differ significantly
330 in their affiliative relationship.

331 Contrary to our expectations, time played no crucial role. It is possible that the trial duration was too
332 long (10s or 40s) to influence subjects' decisions, which were made quickly (mean time to start pulling =
333 0.84s), so there was never any real time pressure despite the salient movement of the dishes. Future
334 studies could investigate whether shorter trial durations influence subjects' responses. Prior to the start
335 of the session subjects could not visually assess the pulling effort required to obtain the rewards but
336 they could experience it at the very first trial of the session and they experienced the same weight in the
337 individual trials just before the test session. Although the pre-test trials were designed to provide this
338 information to the subject and the weights used for each session did not change between the pre-test
339 trials and the test session, it is possible that some subjects did not use this information. It is still an open
340 question whether enabling subjects to explicitly see the different weights involved before engaging with
341 the task might elicit more strategic behaviour.

342 Although chimpanzees mainly cooperated, they differed in the effort they invested when they were
343 tested with different partners. Based on the median latencies of each subject when pulling, all
344 chimpanzee dyads except one initiated their pulling at similar latencies. This result suggests that
345 variation in the amount of weight invested between partners can be better explained by subjects taking
346 into account and adjusting to their partner's behaviour rather than individual variation in latencies to
347 pull (e.g. having quick and slow subjects). Our results are in line with previous evidence which show that
348 chimpanzees can differentiate between their partner's behaviour in cooperative tasks (Melis et al.,
349 2006; Engelmann & Herrmann, 2016).

350 We found that a partner's previous decisions did not have an effect on a subject's likelihood to pull,
351 suggesting that chimpanzees were not taking into account their partner's previous responses to decide
352 whether to pull in a given trial. One possible explanation is that chimpanzees only took into account
353 their partner's current actions, not their past actions. However, their partner's previous responses are

354 not the only information subjects could have used to make their decisions. Their own previous actions as
355 well as the quantity of effort that their partners had invested could have also contributed to their
356 decisions. Alternatively, assuming that they were averse to the risk of losing the rewards, chimpanzees
357 preferred to secure their rewards (by pulling), with the option to adjust how much they pulled.
358 Moreover, chimpanzees also showed signs of strategic decision-making as they waited longer to pull
359 across trials of high weight sessions. Therefore, only in cases where the partners would have been
360 highly reliable, would we expect chimpanzees not to pull and thus completely free-ride as we initially
361 expected. This result helps to explain why they acted strategically by waiting and pulling less weight as
362 second pullers, while still cooperating frequently.

363 When we compared the strategies used by chimpanzees in this study to those human adults employ
364 when they are presented with a snowdrift game, we find that chimpanzees, despite responding flexibly
365 when paired with different partners, do not take into account partner's last actions whereas humans
366 use flexible strategies such as tit-for-tat or Pavlov (Kümmerli et al., 2007). These differences could be
367 due to chimpanzees' aversion to the loss of food rewards (as ultimately one member of the dyad pulled
368 and secured the rewards despite the partner's action) or due to methodological reasons. In fact, human
369 studies are difficult to directly compare with our task because human subjects are usually paired with
370 partners who they do not know or see, they experience real losses, and they cannot decide how much
371 they can invest in the cooperative act as it is generally a binary decision. In contrast, chimpanzees in our
372 study lived in the same group, experienced the loss of potential gains, and were able to decide how
373 much effort they invested in pulling. Future studies are required to compare how non-human primates
374 and developmentally matched human controls behave when presented with the same version of the
375 snowdrift game.

376 Overall, we found that chimpanzees pulled together in most trials (70%) although it was not strictly
377 necessary to get the food. These results are interesting because they are similar to other studies where
378 chimpanzees must cooperate to retrieve their food rewards (Hirata & Fuwa, 2006; Melis et al., 2006,
379 2009). In a cooperative task where subjects faced conflict situation (Melis et al., 2009) cooperation
380 decreased when pairs of chimpanzees pulled for unequal rewards between them, but still were able to
381 cooperate in approximately half of the trials (45%). In the current task, chimpanzees pulled together in a
382 greater proportion of the trials but minimised the costs in the high weight condition (the pulling effort
383 was not the same for each subject). In contrast to Melis et al. (2009), in our task cooperation was not
384 required to obtain the rewards but they still pulled together.

385 Moreover, Bullinger et al. (2011) found that chimpanzees preferred to work alone rather than with a
386 partner to obtain the same rewards in a cooperative task. In contrast, we found that chimpanzees,
387 despite having the option to work alone (by only one subject pulling), often still preferred to pull with
388 their partner rather than free-ride to obtain the same rewards. Perhaps the difference between both
389 studies is that in our task both chimpanzees interact with the same apparatus and therefore social
390 facilitation in combination with the uncertainty of losing rewards if no one pulls, could have helped to
391 maintain the high levels of cooperation we found. In Bullinger et al. (2011) the subject had a clear
392 alternative to work alone and completely avoid the risk of defection by the partner (i.e. the partner
393 refusing to pull). In the current task there is no risk associated with cooperation because chimpanzees
394 can solve the task alone. However, free-riding comes with a slight risk that no one pulls. Thus
395 chimpanzees can remove the risk completely by always pulling (and as a consequence increasing their
396 costs) or they can remove the costs by free-riding and risk losing the rewards if no-one pulls.

397 Therefore, if a partner is required to access the rewards in a cooperative task and no other solution is
398 available, chimpanzees cooperate (Hirata & Fuwa, 2007; Melis et al., 2009). When the partner is not

399 needed and an individual option providing the same rewards is available, chimpanzees prefer to work
400 alone (Bullinger et al., 2011), avoiding the risk of defection by the partner in the cooperative task.
401 However, in our task where cooperation is not necessary to obtain a reward, chimpanzees still
402 cooperate in many trials. These contradictory results can be reconciled if we consider them in terms of
403 risk avoidance and cost reduction. In Bullinger et al. (2011) chimpanzees prefer to work alone to avoid
404 the risk of defection by the partner. In the current study subjects avoid the risk by pulling more often
405 (and thus cooperating) but reduce costs by waiting for the partner and pulling less.

406 The aim of the current experiment was to present chimpanzees with the type of decision they would
407 need to make to coordinate in the wild when conflicts of interest between group members are involved;
408 as in border patrols (Watts & Mitani, 2001) or group hunting (Boesch, 1994, 2002 although see Gilby et
409 al., 2015; Tomasello, 2009 for other interpretations). In these situations, some individuals could
410 potentially reap the benefits of group living without the need to cooperate as long as one or a few
411 others pay the costs (e.g. being the first to start the chase or defend the boundaries of the group range).
412 Moreover, in these situations each subject can potentially adjust their degree of investment and
413 minimise costs while maintaining successful coordination as we have observed in this study.
414 Nevertheless, we are aware that our version of the snowdrift game is a simplified version of real life
415 situations. The main difference is that we apply a 2-person version of the snowdrift game (Sudgen,
416 1986) while chimpanzee hunting (or border patrol) involves usually more than two individuals, and could
417 thus be interpreted as a collective action problem (Kitchen & Beehner, 2007; Nunn, 2000). Some
418 evidence (Schneider et al., 2012) suggests that chimpanzees can solve a collective action problem
419 although it is still not clear whether individuals that started the action are motivated to help their
420 partners (acting as volunteers) or rather due to the higher probabilities to obtain a valuable reward
421 despite performing the action. In fact, dominant individuals resulted in active volunteers presumably
422 because they could obtain the majority of the rewards after volunteering

423 In summary, in a task where free-riding was possible, subjects chose to cooperate in most trials, though
424 there were indications of strategic behaviour. Chimpanzees are capable of cooperating in some
425 situations involving a conflict of interest by managing the trade-off between maintaining successful
426 coordination within the time limits and minimising costs.

427

428

429

430

431

432

433

434

435

436

437

438

439

440

441

442

443

444 **Acknowledgments**

445 We thank R. Piesek and S. Schütte for building the apparatuses; C. Stephens and R. Mundry for their
446 statistical support; Marike Schreiber for the apparatus figure; Manuel Bohn for his insightful comments;
447 the students at the WKPRC for help with data collection and the animal caretakers and chimpanzees for
448 their cooperation. A. Sánchez-Amaro was partially supported by a LaCaixa-DAAD grant (13/94418). J.
449 Call was partially supported by an ERC-Synergy grant SOMICS.

450 We have no competing interests.

451

452

453

454

455

456

457

458

459

460

461

462

463 **References**

- 464 Axelrod, R., & Hamilton, W.D. (1981). The evolution of cooperation. *Science*, *211*, 1390-1396. (doi:
465 10.1126/science.7466396).
- 466 Baayen, R.H., Davidson, D.J., & Bates, D.M. (2008) Mixed-effects modelling with crossed random
467 effects for subjects and items. *Journal of Memory and Language*, *59*, 390-412.
468 (doi:10.1016/j.jml.2007.12.005).
- 469 Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory
470 hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*, 255-278.
471 (doi:10.1016/j.jml.2012.11.001).
- 472 Bates, D.M. *lme4: Mixed-effects modeling with R*. URL <http://lme4.r-forge.r-project.org/book>, 2010.
- 473 Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, *48*, 653-657. (doi:
474 10.1006/anbe.1994.1152).
- 475 Boesch, C. (2002). Cooperative hunting roles among Tai chimpanzees. *Human Nature*, *13*, 27-46. (doi:
476 10.1007/s12110-002-1013-6)
- 477 Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., & Normand, E. (2008). Intergroup
478 conflicts among chimpanzees in Tai National Park: lethal violence and the female perspective.
479 *American Journal of Primatology*, *70*, 519-532. (doi: 10.1002/ajp.20524).
- 480 Bullinger, A., Melis, A., & Tomasello, M. (2011). Chimpanzees, *Pan troglodytes*, prefer individual over
481 collaborative strategies towards goals. *Animal Behaviour*, *82*, 1135-1141.
482 (doi:10.1016/j.anbehav.2011.08.008)
- 483 Chalmeau, R. (1994). Do chimpanzees cooperate in a learning task?. *Primates*, *35*, 385-392.
484 (doi:10.1007/BF02382735)

485 Cronin, K., Bridget, A., van Leeuwen, E., Mundry, R., & Haun, D. (2013). Problem solving in the
486 presence of others: how rank and relationship quality impact resource acquisition in chimpanzees
487 (Pan troglodytes). *PLoS one*, 9, e93204. (doi: 10.1371/journal.pone.0093204)

488 Doebeli, M., & Hauer, C. (2005). Models of cooperation based on the Prisoner's Dilemma and the
489 Snowdrift Game. *Ecology Letters*, 8, 748-766. (doi: 10.1111/j.1461-0248.2005.00773.x).

490 Duffy, J., & Feltovich, N. (2002). Do actions speak louder than words? An experimental comparison of
491 observation and cheap talk. *Games and Economic Behavior*, 38, 1-27. (doi:10.1006/game.2001.0892).

492 Duffy, J., & Feltovich, N. (2006). Words, deeds and lies: strategic behaviour in games with multiple
493 signals. *The Review of Economic Studies*, 669-688. (doi: 10.1111/j.1467-937X.2006.00391.x).

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

497 Engelmann, J. M., & Herrmann, E., (2016). Chimpanzees trust their friends. *Current Biology*, 26, 1-5.
498 (doi: 10.1016/j.cub.2015.11.037).

499 Field, A. (2005) *Discovering Statistics using SPSS*. Sage Publications. London.

500 Galloway, A. T., Addessi, E., Frigaszy, D. M., & Visalberghi, E. (2005). Social facilitation of eating
501 familiar food in tufted capuchins (*Cebus apella*): does it involve behavioral coordination?.
502 *International Journal of Primatology*, 26, 181-189 (doi: 10.1007/s10764-005-0729-7)

503 Gilby, I. C., & Connor, R. C. (2010). The role of intelligence in group hunting: are chimpanzees
504 different from other social predators. In E.V. Lonsdorf, S.R. Ross, & Matsuzawa, T (Eds.), *The mind of*
505 *the chimpanzee: ecological and experimental perspectives* (pp. 220-233). Chicago, IL: The University
506 of Chicago Press.

507 Gilby, I.C., Machanda, Z.P., Mjungu, D.C., Rosen, J., Muller, M. N., Pusey, A. E., & Wrangham, R. W.
508 (2015). "Impact hunters" catalyse cooperative hunting in two wild chimpanzee communities.
509 *Philosophical Transactions of the Royal Society B*, 370, 20150005 (doi: 10.1098/rstb.2015.0005).

510 Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. W. (2007). Tolerance allows bonobos
511 to outperform chimpanzees on a cooperative task. *Current Biology*, 17, 619-623. (doi:
512 10.1016/j.cub.2007.02.040).

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

515 Kitchen, D. M., & Beehner, J. C. (2007). Factors affecting individual participation in group-level
516 aggression among non-human primates. *Behaviour*, 144, 1551-1581. (doi:
517 10.1163/156853907782512074).

518 Kümmerli, R., Colliard, C., Fietcher, N., Petitpiere, B., Russier, F., & Keller, L. (2007). Human
519 cooperation in social dilemmas: comparing the Snowdrift game with the Prisoner's Dilemma.
520 *Proceedings of the Royal Society of London B: Biological Sciences*, 274, 2965-2970. (doi:
521 10.1098/rspb.2007.0793).

522 Kun, A., Boza, G., & Scheuring, I. (2006). Asynchronous snowdrift game with synergistic effect as a
523 model of cooperation. *Behavioural Ecology*, 17, 633-641. (doi: 10.1093/beheco/ark009).

524 Maynard-Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge, UK: Cambridge University
525 Press.

526 Melis, A., Hare, B., & Tomasello, M. (2006) Engineering cooperation in chimpanzees: Tolerance
527 constraints on cooperation. *Animal Behaviour*, 72, 275-286. (doi:10.1016/j.anbehav.2005.09.018).

528 Melis, A., Hare, B., & Tomasello, M. (2009). Chimpanzees coordinate in a negotiation game. *Evolution*
529 *and Human Behaviour, 30*, 381-392. (doi:10.1016/j.evolhumbehav.2009.05.003).

530 Nunn, C. L. (2000). Collective benefits, free-riders, and male extra-group conflict. In P.M. Kappeler
531 (Ed.), *Primate Males: causes and consequences of variation in group composition* (pp. 192-204).
532 Cambridge, UK: Cambridge University Press.

533 Rapoport, A., & Chammah, A. M. (1966). The game of chicken. *American Behavioral Scientist, 10*, 10-
534 28, (doi: 10.1177/000276426601000303).

535 Scheel, D., & Packer, C. (1991). Group hunting behaviour of lions: a search for cooperation. *Animal*
536 *Behaviour, 41*, 697-709. (doi: 10.1016/S0003-3472(05)80907-8).

537 Schneider, A.C., Melis, A., & Tomasello (2012). How chimpanzees solve collective action problems.
538 *Proceedings of the Royal Society of London B: Biological Sciences, 279*, 4946-4954, (doi:
539 10.1098/rspb.2012.1948).

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

542 Sudgen, R. (1986). *The Economics of Rights, Cooperation and Welfare*. Oxford, UK: Basil Blackwell.

543 Tomasello, M. (2009). *Why we cooperate?*. Cambridge, MA: MIT Press.

544

545

546

547

548 **Appendix**

549 **Apparatus characteristics**

550 Chimpanzees pulled in a tray attached to a central weight. The weight was created by the friction of a
551 pair of brakes connected to a training-bike wheel (23 cm of diameter). The brakes could be adjusted by
552 the experimenter thereby adjusting the effort that was needed to move the wheel.

553 The apparatus consisted on a tray (54.5 X 24 cm) positioned on a fixed table (62.5x50 cm). A pair of
554 ropes was connected to the tray. Chimpanzees could pull the ropes and move the tray towards the mesh
555 (movement 1 in Fig. A1).

556 The food was placed on two small dishes (10x10 cm). These dishes could be moved towards the end of
557 the apparatus (at which the food became unavailable) by pulling from a wire that the experimenter
558 controlled (movement 2 in Fig. A2). See figures A1 and A2 for clarification of the apparatus
559 characteristics.

560 We used a metallic barrier (10X194X109 cm) to separate subjects inside the testing room. This barrier
561 was perpendicular to the frontal mesh of the apes' enclosure. With the barrier, both apes were semi-
562 separated so that chimpanzees could not go directly from one side of the room to the other and they
563 could not reach the partners' rewards.

564 **Coding**

565 In this study we measured two variables: the timing of the decisions to pull and the outcomes of apes'
566 actions.

567 The timing was measured from the time the bananas were baited (when chimpanzees were not pulling
568 while we baited the dishes and the peg was already released) or alternatively, when the peg was

569 detached until the first subject started to pull (when chimpanzees were already pulling before the food
570 was baited). We calculated this latency counting the frames (25 fps) until a number equal or higher than
571 1.5 kg was shown in the scale. We removed the weights below 1.5 kg to avoid the noise produced when
572 subjects were just holding the rope and thus only consider instances of active pulling.

573 To obtain the outcomes measures, we calculated the average of the weights (higher than 1.5 kg) shown
574 on the scales while the subjects were pulling from their ropes. We then divided the averages difference
575 between subjects by the sum of both averages. Therefore, we obtained a “measure of equality” (ME),
576 ranging from -1 to 1. We transformed all of the values to positive values for analysis $(1 - \frac{\sum W_1 - \sum W_2}{\sum W_1 + \sum W_2})$. For
577 model 6 we used as a response the percentage of weight that the 1st puller (his average) pulled divided
578 by the total weight pulled by both subjects (the sum of their averages).

579 For model 9 we created an index that took into account all the previous trials within a session that a
580 partner had pull. The index ranged from 0 (no pull in all previous trials) to 1 (pull in all previous trials).

581 **Model analyses**

582 All analyses were conducted using Linear Mixed models (LMM) and Generalized Linear Mixed Models
583 (GLMM) (Baayen, Davidson & Bates, 2008) and were run using R statistics (version 3.1.1) and lme4
584 package (Bates, 2010). We ran all LMM with Gaussian error structure and identity link function and all
585 GLMM with binomial structure and logit link function. All continuous variables were z-transformed. All
586 full models were compared to a null model excluding all the test variables. In order to obtain the p-
587 values for the individual fixed effects we conducted likelihood-ratio tests (Barr et al., 2013).

588 When we analysed the data, one trial was removed due to a problem with the scales and another was
589 missing due experimenter error. Thus the total number of data points was 702 instead of 704.

590 For every model, we assessed model stability by comparing the estimates derived by a model based on
591 all data with those obtained from models with the levels of the random effects excluded one at a time.
592 All models were stable. Moreover, to rule out collinearity we checked Variance Inflation Factors (VIF)
593 (Field, 2005). All VIF values were closer to 1 (maximum VIF across all models = 1.189). In linear mixed
594 models is not possible to obtain effect sizes for each predictor. It is only possible to report size effects
595 for the effect sizes as a whole (or fixed and random effects together). We consider these general effect
596 sizes not informative for the purpose of this study and therefore we do not report them.

597 **Models**

598 **Model 1. Waiting time before pulling (LMM)**

599 Model 1 investigated the length of time subjects waited before acting. In this model we included only
600 the trials where both subjects waited before we released the security peg ($N = 586$). The response was
601 the time (in seconds) that subjects waited before start pulling. We expected subjects to minimise their
602 own effort by waiting longer in high weight than in low weight conditions and that this strategy could
603 increase across trials and sessions. We also expected the type of trial to influence in the subjects waiting
604 time, decreasing their time when in short time trials. We included phase to test whether subjects would
605 wait more in phase 2 due to their previous experience in the task (during phase 1). The full model
606 included the test variables weight condition, type of trial, session, trial and phase as well as the
607 interactions: type of trial, session and trial, each with weight condition. The control variables were: sex
608 of the dyad as fixed effect; subject and dyad as random effects and the random slopes. The full model
609 including all random slopes did not converge, therefore we checked for random slopes that had a
610 minimal effect and we removed them (see Table A2). The comparison between the full and the null
611 model was significant GLMM: $\chi^2_8 = 17.004$, $P = 0.03$, $N = 586$). We dropped the two non-significant
612 interactions from the model: weight condition*type of trial (LMM: $\chi^2_1 = 0.066$, $P = 0.797$, $N = 586$) and

613 weight condition*session number (LMM: $\chi^2_1 = 0.556$, $P = 0.456$, $N = 586$). We found a significant
614 interaction between weight condition*trial: subjects waited longer to pull at the end of high weight
615 sessions (see Table A3).

616 Plotting the overall latencies of each subject (Fig. 3) suggests that the differences we see between
617 partners could not only be explained by individual differences in pulling latencies. However, the dyad
618 Robert-Riet differed in their overall pulling latencies. In this dyad could be that one subject (Riet) never
619 had the opportunity to pull, casting doubt on whether she actively decided to act differently between
620 subjects or the effects were driven by her slow reactions when pulling. In the rest of dyads ($N=9$) there
621 were no overall latency differences.

622 **Model 2. Waiting time before pulling in pre-test trials (LMM)**

623 Model 2 investigated whether subjects differed in their waiting time (measured in seconds) between
624 weight conditions when they were participating in the pre-test trials. The response was the time (in
625 seconds) that subjects waited before start pulling in the pre-test trials. This test was conducted to
626 determine whether subjects were influenced by the weight condition when no partner was present. We
627 hypothesize that subjects will not differ in their latency between weight conditions in those situations.
628 We only took into account the second trial of each pair of experience trials before the start of the test
629 session. The full model included weight condition and session as test variables; sex of the individuals as
630 fixed effect; subject, partner and dyad as random effects and the random slopes (see Table A2). The
631 comparison between the full and the null model was not significant (GLMM: $\chi^2_2 = 1.265$, $P = 0.26$, $N =$
632 166) suggesting that subjects did not differ between weight conditions when they were alone (see Table
633 A4).

634 **Model 3. Time spent pulling by at least one subject, after wait (LMM)**

635 Model 3 investigated the time that subjects spent pulling on the rope within a trial, either individually or
636 simultaneously. In this model we included only the trials where both subjects waited before we released

637 the security peg ($N = 586$). As a response variable we used the total time (measured in seconds) from
638 the moment they started to pull until one chimpanzee touched a piece of banana. If chimpanzees were
639 getting tired across the trials of a high weight session, we would expect them to pull more slowly
640 towards end of the sessions. We would expect them to pull faster in low weight trials overall and to not
641 change their time spent pulling within a session. The full model included the test variables weight
642 condition, type of trial, session and trial as well as the interactions: type of trial, session and trial, each
643 with weight condition. The control variables were phase and sex of the dyad as fixed effects; subject and
644 dyad as random effects and the random slopes (see Table A2). The comparison between the full and the
645 null model was significant (LMM: $\chi^2_8 = 32.73$, $P < 0.0001$, $N = 586$). We dropped the two non-significant
646 interactions from the model: weight condition*type of trial (LMM: $\chi^2_1 = 2.177$, $P = 0.14$, $N = 586$) and
647 weight condition*session number (LMM: $\chi^2_1 = 0.013$, $P = 0.909$, $N = 586$). We found a significant
648 interaction between weight condition*trial suggesting that subjects got slightly faster across high weight
649 sessions (See Table A5).

650 **Model 4. Likelihood to cooperate (GLMM)**

651 Model 4 investigated the each dyad's likelihood to pull together. In this model we included all the data
652 ($N = 702$). We transform our response (ME) into a binomial response where 1 meant both pulling and 0
653 meant that only one subject pulled. We expected cooperation to increase across trials and/or sessions.
654 We expected subjects to pull together more often in high weight trials. We also expected the type of
655 trial to influence subjects in their likelihood to pull together, pulling together more often in short time
656 trials. We included phase to test whether subjects would cooperate more in phase 2 due to their
657 previous experience in the task (during phase 1). The full model included the test variables weight
658 condition, type of trial, session, trial and phase as well as the interactions: type of trial, session and trial,
659 each with weight condition. The control variables were: sex of the dyad and the total time until the
660 subjects touches the reward as fixed effect; subject and dyad as random effects and the random slopes
661 (see Table A2). The comparison between the full and the null model was marginally significant (GLMM:
662 $\chi^2_8 = 13.457$, $P = 0.097$, $N = 702$). Therefore, due to the observed trend ($p < 0.1$) we inspected how the

663 test variables contributed to the response. We dropped the two non-significant interactions from the
664 model: weight condition*type of trial (GLMM: $\chi^2_1 = 0.314$, $P = 0.575$, $N = 702$) and weight condition*trial
665 number (GLMM: $\chi^2_1 = 0.106$, $P = 0.745$, $N = 702$). We found an almost significant interaction between
666 these two variables suggesting that subjects pulled together more often during the last high weight
667 sessions (see Table A6).

668 **Model 5. Degree of cooperation (LMM)**

669 Model 5 investigated the dyad's degree of cooperation. The response of the model was the ME (see
670 coding section above). In the model we only take into account the dyads pulled together ($N = 490$). We
671 expected subjects to cooperate more in high weight condition (especially in short time trials where the
672 risk of losing the reward were higher). At the same time we expected cooperation to increase across
673 sessions and/or trials in high weight trials as a consequence of experience pulling together. In contrast,
674 in low weight trials we expected subjects not to coordinate that often as they could easily pull alone.
675 The full model included the test variables weight condition, type of trial, session, trial and phase as well
676 as the interactions: type of trial, session and trial, each with weight condition. The control variables
677 were: sex of the dyad as fixed effect and subject and dyad as random effects. The random slopes of this
678 model and the subsequent models are described in Table A2. The comparison between the full and the
679 null model was not significant (LMM: $\chi^2_8 = 9.716$, $P = 0.286$, $N = 490$) indicating that the test variables did
680 not significantly contribute to the subjects degree of cooperation (see Table A7).

681 **Model 6. Difference in weight between 1st and 2nd puller (LMM)**

682 Model 6 investigated the percentage of the total weight pulled by the first puller (excluding trials in
683 which only the first subject pulled ($N = 212$) and trials where both subjects pulled at the same time ($N =$
684 12). The response was the percentage of weight pulled by the first puller. We expected that the first

685 puller would pull a higher weight than the second puller. Moreover, despite pulling together more in the
686 high weight condition, we expect that the differences between both subjects might increase across high
687 weight sessions because subjects would increasingly try to avoid pulling first (the most costly). The full
688 model included the test variables weight condition, type of trial, session, trial and phase as well as the
689 interactions: type of trial, session and trial, each with weight condition. The control variables were: sex
690 of the dyad, phase, type of trial, trial and session as fixed effects; subject and dyad as random effects
691 and the random slopes (see Table A2). The comparison between the full and the null model was
692 significant (LMM: $\chi^2_4 = 10.268$, $P = 0.031$, $N = 478$). We dropped the two non-significant interactions from
693 the model: weight condition*type of trial (LMM: $\chi^2_1 = 1.074$, $P = 0.3$, $N = 478$) and weight condition*trial
694 number (LMM: $\chi^2_1 = 0.0009$, $P = 0.976$, $N = 478$). We found a significant interaction between weight
695 condition*session: the 1st puller pulled more weight in later sessions of the high weight (see Table A8).

696 **Differences between model 5 and model 6**

697 These two models, despite answering similar questions differ substantially in their response. Model 5 is
698 not directional and measures the equality of cooperation between both individuals pulling while Model
699 6 is directional as it takes the percentage of the total weight pulled by the 1st puller compared to the 2nd
700 puller as the response, answering the specific question of how much weight was pulled by the subject
701 that initiated the action compared to the subject that lagged behind. We ran Model 3 in order to assess
702 whether there was indeed a cost to being the first puller.

703 **Model 7. Difference in weight pulled regarding the partners (LMM)**

704 Model 7 investigated whether subjects performed differently (with regard to the average weight pulled)
705 with the two partners they were tested with. As a response we used the difference in weight that the
706 subjects moved when they were paired with different partners. To calculate the response we previously

707 calculated the total average weight that each subject moved across all sessions with a specific partner
708 and then the difference between those average values. Therefore we obtained 20 responses; each was
709 the difference in weight for the subject's response between the two partners for each condition. The full
710 model included weight condition as fixed factor and subject as random effect. The comparison between
711 the full and the null model was not significant (GLMM: $\chi^2_1 = 0.268$, $P = 0.605$, $N = 20$). Moreover, we
712 investigated whether there was a general tendency, regardless of the condition, for subject's differing in
713 their average pulled weight when confronted with different partners. Due to the nature of GLMM we
714 were unable to calculate the p-value to accompany the results. Instead, we use a bootstrapping
715 (boot.glm function) to calculate the CI. We see that subject's rates of pulled weight differed significantly
716 from 0 (no difference in subject's response in relation to weight between different partners) ($X = 45.77$,
717 CI [28.92, 63.12]) suggesting that they were moving significantly different amounts of weight when they
718 were paired with different partners.

719 **Model 8. Previous experience effect on cooperation in subsequent trials (GLMM).**

720 Model 8 investigated whether subjects' probability of the subject to pull was influenced by the partners'
721 previous decisions to pull within a session. In this model we excluded the first trial of each session, as
722 subjects had no previous experience before that trial. Therefore, we only used data were subjects had
723 previous experience with a partner. As a response we used the ME index. We expected that the
724 likelihood to pull would have been constant regardless of the partners' previous decisions to pull.
725 However, in the extreme cases where the partners would have been very reliable, we would have
726 expected subjects to pull less. We also expected the type of trial to influence subjects' likelihood to pull,
727 pulling more often in short time trials in order to secure the rewards. The full model included the test
728 variables, weight condition, type of trial, session, trial and phase as well as the interactions: type of trial,
729 session, trial and previous experience each with weight condition. The control variables were: sex of the

730 dyad, phase, type of trial, trial, session and the total time until the subjects touches the reward as fixed
731 effect; subject and dyad as random effects and the random slopes (see Table A2). The comparison
732 between the full and the null model was non-significant (GLMM: $\chi^2_8 = 6.202$, $P = 0.4$, $N = 1228$) (see Table
733 A9).

734 **Model 9. Likelihood to wait before pulling (GLMM)**

735 Model 9 investigated the subject's likelihood to wait or not before pulling. In this model we included all
736 the data ($N = 702$). We transformed the response (latency in seconds) into a binomial response (*wait*
737 and *not wait*). We expected that subjects would wait more often in high weight than in low weight and
738 that the proportion of times that subjects waited would increase across trials and sessions. The full
739 model included the test variables weight condition, type of trial, session, trial and phase as well as the
740 interactions: type of trial, session and trial, each with weight condition. The control variables were: sex
741 of the dyad as fixed effect; subject and dyad as random effects and the random slopes (see Table A2).
742 The comparison between the full and the null model was not significant (GLMM: $\chi^2_8 = 7.374$, $P = 0.497$, N
743 = 702) indicating that the test variables did not significantly contribute to the subjects likelihood to wait
744 (see Table A10).

745

746

747

748

749

750

751

752

753

754

755

756

757

758

759

760

761

762

763

764

765

766

767

768

769 Table 1

770 Models conducted in the study (LMM: linear mixed model; GLMM: generalized linear mixed model).

771 Random slopes are shown in the Appendix Table A2.

Models	Type	Response	Fixed factors	Random effects
1	LMM	Latency to pull	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2) and sex of the dyad (male, female or mix)	Dyad and subject
2	LMM	Latency in precondition trials	Condition (low and high weight), session (1-8) and sex of individual (male, female)	Subject, partner and dyad
3	LMM	Time spent pulling	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2) and sex of the dyad (male, female or mix)	Dyad and subject
4	GLMM	Pull together or not	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2), total time of trial and sex of the dyad (male, female or mix)	Dyad and subject
5	LMM	Weight ratio	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2) and sex of the dyad (male, female or mix)	Dyad and subject
6	LMM	Proportion of first puller	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2) and sex of the dyad (male, female or mix)	Dyad and subject
7	LMM	Inequality in weight between partners	Condition (low and high weight)	Subject
8	GLMM	Subject pull	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2), total time of trial, previous experience and sex of dyad (male, female or mix)	Dyad, subject, partner and trial id.

772

773

774

775

776

777

778 Table A1. Subject's information

Name	Sex	Age (years)	Paired with (phase 1)	Paired with (phase 2)	Relationship (phase 1)	Relationship (phase 2)
Lobo	M	10	Kara	Kofi	Paternal half siblings	Paternal half siblings
Kara	F	9	Lobo	Sandra	Paternal half siblings	Paternal half siblings
Lome	M	13	Frodo	Robert	Paternal half siblings	Father-son
Robert	M	39	Riet	Lome	Non-kin	Father-son
Frodo	M	21	Lome	Riet	Paternal half siblings	Non-kin
Kofi	M	9	Ulla	Lobo	Mother-Son	Paternal half siblings
Sandra	F	21	Tai	NA	Full siblings	
Tai	F	12	Sandra	NA	Full siblings	
Riet	F	37	Robert	Frodo	Non-kin	Non-kin
Ulla	F	34	Kofi	Corrie	Mother-Son	Paternal half siblings
Fraukje	F	38	Corrie	Kara	Non-kin	Mother- daughter
Corrie	F	38	Fraukje	Ulla	Non-kin	Paternal half siblings

779 Table A2. Model information (below)

Models	Type	Response	Fixed factors	Random effects	Random slopes
1	LMM	Latency to pull	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2) and sex of the dyad (male, female or mix)	dyad and subject	Session-dyad, session-subject right, session-subject left, trial-dyad, trial-subject right, trial-subject left, condition-dyad, condition-subject right, condition-subject left, type of trial-dyad, type of trial-subject right, type of trial-subject left, phase-subject right, phase-subject left, condition*type of trial-dyad, condition*type of trial-subject right, condition*type of trial-subject left, condition*session-dyad, condition*session-subject right, condition*session-subject left, condition*trial-subject right, condition*trial-subject left
2	LMM	Latency in precondition trials	Condition (low and high weight), session (1-8) and sex of individual (male, female)	subject, partner and dyad	Condition-subject, condition-partner, condition-dyad, session-subject, session-partner, session-dyad
3	LMM	Time spent pulling	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2) and sex of the dyad (male, female or mix)	dyad and subject	As in model 1
4	GLMM	Pull together or not	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2), total time of trial and sex of the dyad (male, female or mix)	dyad and subject	Session-dyad, session-subject right, session-subject left, trial-dyad, trial-subject right, trial-subject left, condition-dyad, condition-subject right, condition-subject left, type of trial-dyad, type of trial-subject right, type of trial-subject left, phase-subject right, phase-subject left, total time trial-dyad, total time trial-subject right, total time trial-subject left, condition*type of trial-dyad, condition*type of trial-subject right, condition*type of trial-subject left, condition*session-dyad, condition*session-subject right, condition*session-subject left, condition*trial-subject right, condition*trial-subject left
5	LMM	Weight ratio	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2) and sex of the dyad (male, female or mix)	dyad and subject	As in model 1
6	LMM	Proportion 1st puller	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2) and sex of the dyad (male, female or mix)	dyad and subject	As in model 1
7	LMM	Inequality in weight between partners	Condition (low and high weight)	subject	No random slopes
8	GLMM	Subject pull	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2), total time of trial, previous experience and sex of dyad (male, female or mix)	Dyad, subject, partner and trial id.	Phase-subject, phase-partner, previous experience-subject, previous experience-partner, previous experience-dyad, type of trial-dyad, type of trial-subject, type of trial-partner, session-dyad, session-subject, session-partner, condition-dyad, condition-subject, condition-partner, trial-dyad, trial-subject, trial-partner, total time-dyad, total time-subject, total time-partner, condition*session-dyad, condition*session-subject, condition*session-partner, condition-trial*dyad, condition-trial*subject, condition-trial*partner, condition*previous experience-dyad, condition*previous experience-subject, condition*previous experience-partner
9	GLMM	Likelihood to wait or not	Condition (low and high weight), session (1-8), trial (1-8), type of trial (short-long trials), phase (1-2) and sex of the dyad (male, female or mix)	Dyad and subject	As in model 1

780 Table A3

781 Table Model 1

Test category (reference category)	Estimate	Standard Error	Chi- square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	-0.123	0.158	-	-	-	-0.432/0.197
Phase	0.049	0.099	0.22	1	0.638	-0.123/0.252
Sex of dyad	-	-	0.404	2	0.817	-
Type of trial (long)	-0.034	0.046	0.525	1	0.469	-0.126/0.059
Session number	-0.017	0.054	0.099	1	0.753	-0.122/0.089
Weight condition*trial number	-0.107	0.043	6.127	1	0.013	-0.195/-0.022

782

783

784

785 Table A4

786 Table Model 2

Test category (reference category)	Estimate	Standard Error	CI (95%) of the full model	787 788
Intercept	0.919	0.137	0.641/1.189	789
Sex of the subject (female)	0.197	0.209	-0.231/-0.655	790 791
Weight condition (low)	-0.067	0.059	-0.193/0.056	792
session number	0.034	0.029	-0.019/0.091	793 794

795

796

797

798

799

800

801

802

803 Table A5

804 Table Model 3

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	1.257	0.121	-	-	-	0.999/1.492
Phase	-0.003	0.076	0.002	1	0.968	-0.142/0.158
Sex of dyad	-	-	0.705	2	0.703	-
Type of trial (long)	0.03	0.043	0.493	1	0.483	-0.054/0.115
Session number	-0.07	0.032	3.13	1	0.077	-0.134/ 0.007
Weight condition*trial number	0.119	0.036	10.76	1	0.001	0.047/0.188

805

806

807 Table A6

808 Table Model 4

Test category (reference category)	Estimate	Standard Error	Chi- square	Degrees of freedom	p- value	CI (95%) of the reduced model
Intercept	3.973	0.786	-	-	-	2.847/5.417
Phase	0.543	0.515	0.938	1	0.334	-0.438/1.686
Total time until they touch the reward	0.562	0.258	3.497	1	0.061	0.114/1.199
Sex of dyad	-	-	9.919	2	0.007	-
Type of trial (long)	-0.199	0.237	0.643	1	0.423	-0.725/0.277
Trial number	-0.283	0.168	1.985	1	0.159	-0.670/0.067
Weight condition*session number	-0.967	0.437	3.518	1	0.06	-1.911/-0.108

809

810

811 Table A7

812 Table Model 5

Test category	Estimate	Standard Error	CI (95%) of the full model
Intercept	0.587	0.052	0.470/0.703
Phase	-0.027	0.026	-0.081/0.032
Sex of dyad	-	-	-
Weight condition*Type of trial	-0.046	0.037	-0.116/0.028
Weight condition*Trial number	0.024	0.028	-0.024/0.054
Weight condition*session number	0.017	0.019	-0.03/0.078

813

814

815

816

817

818

819 Table A8

820 Table Model 6

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	0.577	0.0322	-	-	-	0.513/0.647
Phase	0.003	0.013	0.06	1	0.807	-0.026/0.032
Sex of dyad	-	-	2.139	2	0.343	-
Type of trial (long)	-0.043	0.025	2.516	1	0.113	-0.089/0.007
Trial number	-0.006	0.017	0.117	1	0.731	-0.042/0.028
Weight condition*session number	-0.065	0.0212	7.252	1	0.007	-0.103/-0.021

821

822 Table A9

823 Table Model 8

Test category (reference category)	Estimate	Standard Error	CI (95%) of the full model
Intercept	6.954	1.348	17.668/35.504
Phase	0.793	0.952	-1.580/ 3.140
Total time until they touch the reward	0.6	0.421	-0.284/ 3.085
Sex of dyad	NA	-	-
Type of trial (long)	-0.028	0.422	-20.926/ -9.498
Trial number	-0.304	0.223	-1.888/ 0.182
Weight condition (high)	-0.313	0.865	-21.029/-9.506
Session number	0.941	0.722	-0.508/ 3.928
Previous experience	-0.826	1.178	-45.465/-23.530

824

825

826 Table A10

827 Table Model 9

Test category	Estimate	Standard Error	CI (95%) of the full model	828
Intercept	3.822	0.756	2.648/5.673	829
				830
Phase	0.075	-0.332	-0.332/0.507	831
				832
Sex of dyad	NA	-	-	833
				834
Weight condition*Type of trial	-0.552	0.514	-1.641/0.627	835
				836
Weight condition*Trial number	-0.281	0.334	-1.108/0.361	837
				838
Weight condition*session number	0.574	0.302	-0.013/1.239	839
				840

842

843

844 Figure captions

845 **Figure 1.** Experimental set-up. Both chimpanzees can either pull or not from their ropes to move the
846 tray and retrieve the rewards.

847 **Figure 2.** a) Latency to pull the tray in high and low weight conditions across trials; b) Time spent pulling
848 the tray in high and low weight condition across trials after starting the action; c) Proportion of trials
849 that subjects pulled together in high and low weight conditions across sessions and d) Proportion of
850 weight pulled by the first puller across sessions. The dotted-lines represent the fitted-model and the
851 coloured areas represent the CI at 95%.

852 **Figure 3.** Pulling latencies (s) for all subjects.

853 **Figures A1** Apparatus characteristics

854 **Figure A2** Apparatus characteristics

855

856

857

858

859

860

861

862

863 Figures

864 1



865

866

867

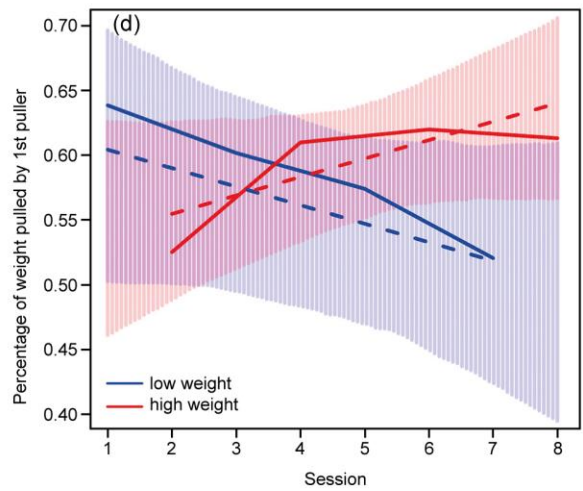
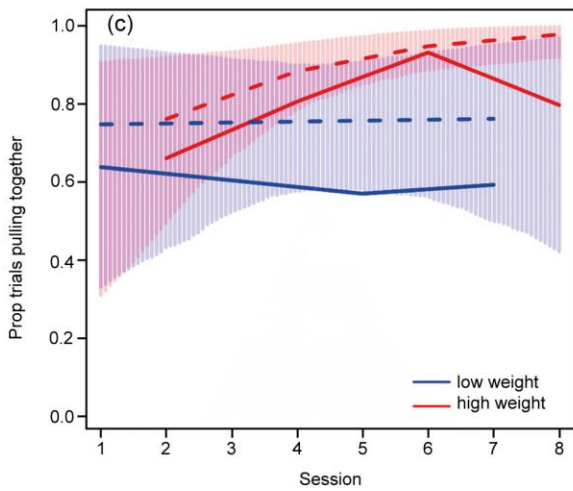
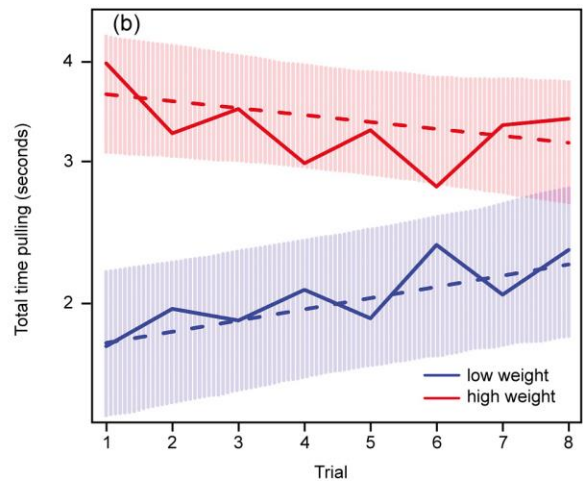
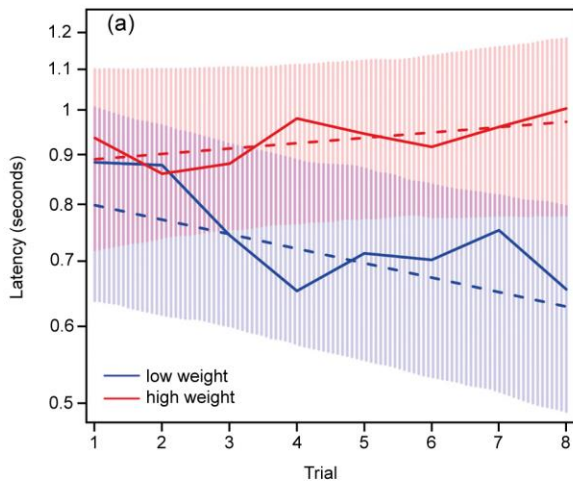
868

869

870

871

872



874

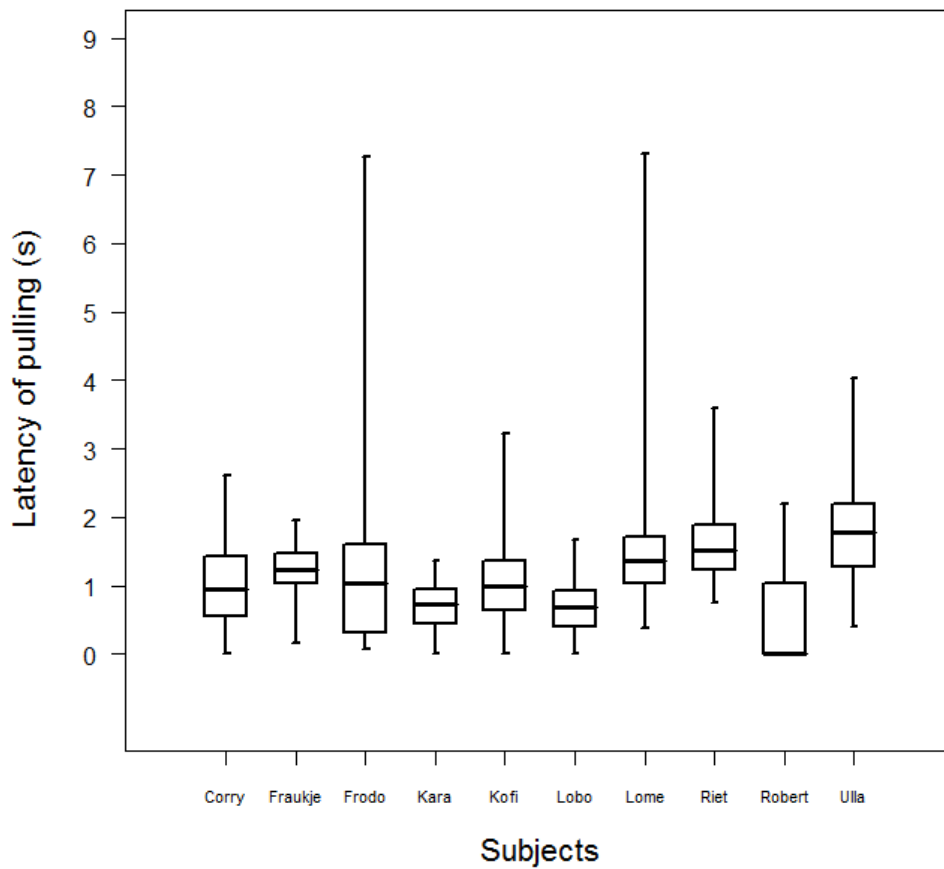
875

876

877

878

879



881

882

883

884

885

886

887

888 A1

889

890

891

892

893

894

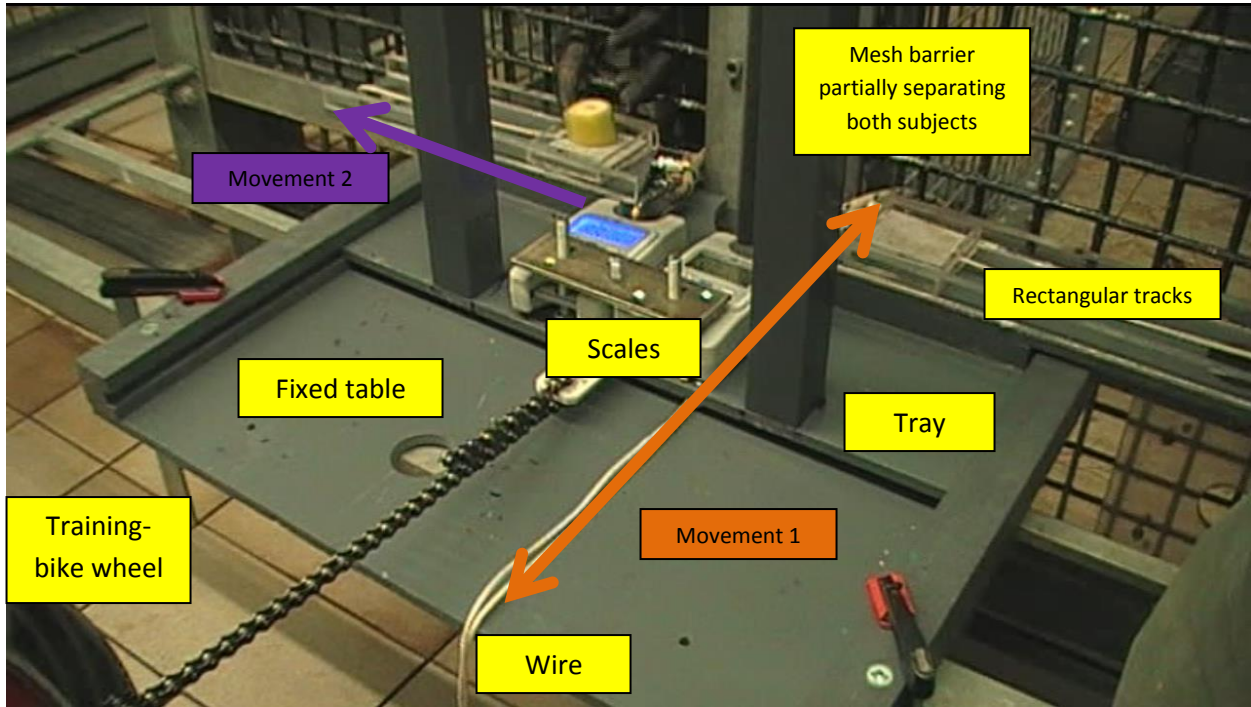
895

896

897

898

899



900 A2

901

