TITLE: Chimpanzees coordinate in a Snowdrift Game.

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Abstract

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

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

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

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

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

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

These types of interactions have been modelled by theorists in the snowdrift game (Doebeli & Hauer, 2005; Kun, Boza & Scheuring, 2006; Sudgen, 1986). In the classic description of the snowdrift situation two cars become stranded on a highway that is covered with snow. The snow must be shovelled off the road before the drivers can return home. They could shovel the snow together and share the work, or alternatively, one driver could do it alone. Each driver would prefer that the other one do it. However, if one of them defects the other should shovel the snow, thus paying the costs to return home. So in the snowdrift dilemma, subjects have a common goal that can be either achieved by performing a cooperative act (either together or individually) or free-riding. Of course, it is in the interest of each subject to defect and let the partner incur the cost but if neither pays the costs both lose. According to recent literature (Kun et al., 2006) chimpanzee hunting could be explained by applying the metaphor of the snowdrift game. Chimpanzees would prefer others to start the hunt unless no one else starts. In the latter case, as in the previous example, the chimpanzee would prefer to begin the hunt rather than let the monkey escape. So, unlike in the prisoner's dilemma (Axelrod & Hamilton, 1981; Maynard-Smith, 1982) acting cooperatively can avoid the worst-case scenario as a cooperative act will always provide a benefit, even for the subject that carries out the costly action.

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

The aim of this study was to use the snowdrift model to investigate how chimpanzees solve a coordination task with a conflict of interest. We presented pairs of chimpanzees with a version of the snowdrift game in which they obtained food rewards by pulling a weighted tray towards them. They could either perform a cooperative act (pull the rope and do all the work or both pull and thus share the load) or one could free-ride while the other did the work. Importantly, chimpanzees were free to decide the amount of weight they pulled. Therefore, cooperation, defined by both individuals pulling during the same trial, could be skewed towards one subject depending on the efforts invested by each member of the dyad. In real-life situations, chimpanzees are able to vary their degree of investment by starting the chase, follow other individuals and join the chase or lag behind and reap the benefits from the hunt (Boesch, 2002; Gilby et al., 2015). For instance, in the case of hunting, chimpanzees could theoretically initiate the hunt but then let others do most of the work, although to our knowledge this has not been empirically demonstrated. Therefore subjects are not only faced with a binomial decision (either cooperate or free-ride) as in previous cooperative games (Chalmeau, 1994; Duguid et al., 2014 Hirata & Fuwa, 2007; Melis et al., 2006, 2009) but can adjust their actions by investing different amounts of effort (i.e. their speediness in chasing the monkey), allowing them to make precise decisions based on the physical contingencies and the partners' actions. In our task both subjects got the same amount of food as long as one individual pulled, so there was no need for cooperation. However, if neither pulled within a certain time-frame both lost the food. This set up reflects the payoffs of the 2-person snowdrift game where the best strategy for a chimpanzee was to wait for the partner to pull and obtain the benefit (b) but pay the cost of the action if the partner did not pull (b-c) to avoid losing the rewards if no one pulls (b = 0). At the same time, if both partners pull simultaneously, that results in an intermediate cooperative strategy where costs are divided (b-c/2).

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

Our main interests were whether chimpanzees a) would maximize their benefit (food – cost of pulling) by waiting for a partner to pull first, b) would solve the task (get the food) by cooperating or free-riding, c) change their strategies with different partners. We manipulated weight and time to approximate the contingencies of chimpanzee hunting: the apes have to overcome the costs to initiate the action (the weight that they have to move) while the prey is only available for a limited time (the time limits). If chimpanzees acted strategically, we expected them to wait longer to pull when the costs of pulling the tray were high (i.e. it was heavy) and for one individual to free-ride more often (understood as not pulling at all) while the other always pulled. In contrast, during low weight trials we expected chimpanzees to pay less attention to their partners' actions and thus wait less to pull. We also expected chimpanzees to wait longer in long time trials as they would have more opportunity to free-ride compared to short time trials. Our study consisted of two phases: all subjects completed the test with one partner first before partners were re-shuffled for a second round. With this manipulation we could study the overall effect of experience and whether they were able to adjust their actions to the behaviour of their partners as they should not only consider the physical contingencies of the task (weight and time) but also their partners' decisions to maximize their rewards and coordinate their actions.

MATERIALS AND METHODS

Subjects

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

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

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

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

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

Individual training

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

Dyadic training

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

Test sessions

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

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

Coding

We measured the outcome of chimpanzees' actions (success/failure), the weight each partner pulled, and the timing of pulling. To evaluate all possible instances of cooperation we calculated a "measure of equality" (ME) based on the weight pulled by both subjects on a given trial. To measure the ME we calculated the average of the weights (higher than 1.5 kg) shown on the scales while the subjects were pulling from their ropes. We then divided the difference between averages of the two subjects by the sum of both averages. Therefore, we obtained a "measure of equality" (ME), ranging from -1 to 1. We transformed all of the values to positive values for analysis. Thus, an ME of 1 indicated perfect cooperation (subjects pulled an equal weight) while 0 indicated complete free-riding (only one individual pulled; see Appendix for further details). Importantly, by using this measure, we could identify the exact degree of cooperation (the investment by each subject). To assess whether subjects waited for a partner to pull we recorded the time between the start of the trial and the first subject of the dyad to pull. This was possible as we recorded all sessions with digital cameras and we could calculate times up to 1/25 of a second (see Appendix for further details). We analysed whether the subjects that were tested in two pairs (N=10) changed their behaviour (based on the weight moved) with different partners. The inter-observer agreement was excellent based on the 15% of the data (R^2 = 0.99) and latencies (R^2 = 0.94).

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

Ethical note

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

RESULTS

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

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

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

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

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

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

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

DISCUSSION

In a task where chimpanzees could potentially free-ride and benefit from their partner's actions, dyads solved the coordination problem by pulling together, with a tendency to pull more often together when those costs were high. However, there were also indications that chimpanzees acted strategically to minimize their effort: they were more likely to wait longer to pull at the end of high weight sessions and the effort invested by first and second puller was imbalanced. Therefore, although chimpanzees did not free-ride (by not pulling at all) more in high weight conditions as we predicted, they did it so in more subtle ways, by investing unequal efforts. Chimpanzees also differed significantly in the effort they invested when tested with different partners.

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

Alternatively, it could be that some chimpanzees were just pulling to obtain the food regardless of the effort and the partners' presence. But if this were true we would not expect to find differences in their latency to pull between conditions. On the contrary, subjects behaved strategically when pulling high weights. Moreover, we would not expect that cooperation tended to increase across sessions when subjects had already experienced in the dyadic training that they could obtain food without pulling, but it increased over time in that condition suggesting that subjects cooperated depending on the effort they were required to contribute and their prior experience.

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

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

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

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

We found that a partner's previous decisions did not have an effect on a subject's likelihood to pull, suggesting that chimpanzees were not taking into account their partner's previous responses to decide whether to pull in a given trial. One possible explanation is that chimpanzees only took into account their partner's current actions, not their past actions. However, their partner's previous responses are not the only information subjects could have used to make their decisions. Their own previous actions as well as the quantity of effort that their partners had invested could have also contributed to their decisions. Alternatively, assuming that they were averse to the risk of losing the rewards, chimpanzees preferred to secure their rewards (by pulling), with the option to adjust how much they pulled. Moreover, chimpanzees also showed signs of strategic decision-making as they waited longer to pull across trials of high weight sessions. Therefore, only in cases where the partners would have been highly reliable, would we expected chimpanzees not to pull and thus completely free-ride as we initially expected. This result helps to explain why they acted strategically by waiting and pulling less weight as second pullers, while still cooperating frequently.

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

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

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

Therefore, if a partner is required to access the rewards in a cooperative task and no other solution is available, chimpanzees cooperate (Hirata & Fuwa, 2007; Melis et al., 2009). When the partner is not needed and an individual option providing the same rewards is available, chimpanzees prefer to work alone (Bullinger et al., 2011), avoiding the risk of defection by the partner in the cooperative task. However, in our task where cooperation is not necessary to obtain a reward, chimpanzees still cooperate in many trials. These contradictory results can be reconciled if we consider them in terms of risk avoidance and cost reduction. In Bullinger et al. (2011) chimpanzees prefer to work alone to avoid the risk of defection by the partner. In the current study subjects avoid the risk by pulling more often (and thus cooperating) but reduce costs by waiting for the partner and pulling less.

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

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

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Appendix

Apparatus characteristics

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

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

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

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

Coding

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

The timing was measured from the time the bananas were baited (when chimpanzees were not pulling while we baited the dishes and the peg was already released) or alternatively, when the peg was detached until the first subject started to pull (when chimpanzees were already pulling before the food was baited). We calculated this latency counting the frames (25 fps) until a number equal or higher than 1.5 kg was shown in the scale. We removed the weights below 1.5 kg to avoid the noise produced when subjects were just holding the rope and thus only consider instances of active pulling.

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

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

Model analyses

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

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

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

Models

Model 1. Waiting time before pulling (LMM)

Model 1 investigated the length of time subjects waited before acting. In this model we included only the trials were both subjects waited before we released the security peg (*N* = 586). The response was the time (in seconds) that subjects waited before start pulling. We expected subjects to minimise their own effort by waiting longer in high weight than in low weight conditions and that this strategy could increase across trials and sessions. We also expected the type of trial to influence in the subjects waiting time, decreasing their time when in short time trials. We included phase to test whether subjects would wait more in phase 2 due to their previous experience in the task (during phase 1). The full model included the test variables weight condition, type of trial, session, trial and phase as well as the interactions: type of trial, session and trial, each with weight condition. The control variables were: sex of the dyad as fixed effect; subject and dyad as random effects and the random slopes. The full model including all random slopes did not converge, therefore we checked for random slopes that had a minimal effect and we removed them (see Table A2).The comparison between the full and the null model was significant GLMM: χ^2_8 = 17.004, *P* = 0.03, *N*= 586). We dropped the two non-significant interactions from the model: weight condition*type of trial (LMM: χ^2_1 = 0.066, *P* = 0.797, *N* = 586) and weight condition*session number (LMM: χ^2_1 = 0.556, *P* = 0.456, *N* = 586). We found a significant interaction between weight condition*trial: subjects waited longer to pull at the end of high weight sessions (see Table A3).

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

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

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

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

Model 3 investigated the time that subjects spent pulling on the rope within a trial, either individually or simultaneously. In this model we included only the trials were both subjects waited before we released the security peg (*N* = 586). As a response variable we used the total time (measured in seconds) from the moment they started to pull until one chimpanzee touched a piece of banana. If chimpanzees were getting tired across the trials of a high weight session, we would expect them to pull more slowly towards end of the sessions. We would expect them to pull faster in low weight trials overall and to not change their time spent pulling within a session. The full model included the test variables weight condition, type of trial, session and trial as well as the interactions: type of trial, session and trial, each with weight condition. The control variables were phase and sex of the dyad as fixed effects; subject and dyad as random effects and the random slopes (see Table A2). The comparison between the full and the null model was significant (LMM: χ^2_8 = 32.73, P < 0.0001, N = 586). We dropped the two non-significant interactions from the model: weight condition*type of trial (LMM: χ^2_1 = 2.177, P = 0.14, N = 586) and weight condition*session number (LMM: χ^2_1 = 0.013, P = 0.909, N = 586). We found a significant interaction between weight condition*trial suggesting that subjects got slightly faster across high weight sessions (See Table A5).

Model 4. Likelihood to cooperate (GLMM)

Model 4 investigated the each dyad's likelihood to pull together. In this model we included all the data (*N* = 702). We transform our response (ME) into a binomial response where 1 meant both pulling and 0 meant that only one subject pulled. We expected cooperation to increase across trials and/or sessions. We expected subjects to pull together more often in high weight trials. We also expected the type of trial to influence subjects in their likelihood to pull together, pulling together more often in short time trials. We included phase to test whether subjects would cooperate more in phase 2 due to their previous experience in the task (during phase 1). The full model included the test variables weight condition, type of trial, session, trial and phase as well as the interactions: type of trial, session and trial, each with weight condition. The control variables were: sex of the dyad and the total time until the subjects touches the reward as fixed effect; subject and dyad as random effects and the random slopes (see Table A2). The comparison between the full and the null model was marginally significant (GLMM: χ^2_8 = 13.457, P = 0.097, N = 702). Therefore, due to the observed trend (p< 0.1) we inspected how the test variables contributed to the response. We dropped the two non-significant interactions from the model: weight condition*type of trial (GLMM: χ^2_1 = 0.314, *P* = 0.575, *N* = 702) and weight condition*trial number (GLMM: χ^2_1 = 0.106, *P* = 0.745, *N* = 702). We found an almost significant interaction between these two variables suggesting that subjects pulled together more often during the last high weight sessions (see Table A6).

Model 5. Degree of cooperation (LMM)

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

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

Model 6 investigated the percentage of the total weight pulled by the first puller (excluding trials in which only the first subject pulled (*N* = 212) and trials where both subjects pulled at the same time (*N* = 12). The response was the percentage of weight pulled by the first puller. We expected that the first puller would pull a higher weight than the second puller. Moreover, despite pulling together more in the high weight condition, we expect that the differences between both subjects might increase across high weight sessions because subjects would increasingly try to avoid pulling first (the most costly). The full model included the test variables weight condition, type of trial, session, trial and phase as well as the interactions: type of trial, session and trial, each with weight condition. The control variables were: sex of the dyad, phase, type of trial, trial and session as fixed effects; subject and dyad as random effects and the random slopes (see Table A2). The comparison between the full and the null model was significant (LMM: χ^2_4 = 10.268, *P* = 0.031, *N* = 478). We dropped the two non-significant interactions from the model: weight condition*type of trial (LMM: χ^2_1 = 1.074, *P* = 0.3, *N* = 478) and weight condition*trial number (LMM: χ^2_1 = 0.0009, *P* = 0.976, *N* = 478). We found a significant interaction between weight condition*session: the 1st puller pulled more weight in later sessions of the high weight (see Table A8).

Differences between model 5 and model 6

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

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

Model 7 investigated whether subjects performed differently (with regard to the average weight pulled) with the two partners they were tested with. As a response we used the difference in weight that the subjects moved when they were paired with different partners. To calculate the response we previously calculated the total average weight that each subject moved across all sessions with a specific partner and then the difference between those average values. Therefore we obtained 20 responses; each was the difference in weight for the subject's response between the two partners for each condition. The full model included weight condition as fixed factor and subject as random effect. The comparison between the full and the null model was not significant (GLMM: χ^2_1 = 0.268, P = 0.605, N = 20). Moreover, we investigated whether there was a general tendency, regardless of the condition, for subject's differing in their average pulled weight when confronted with different partners. Due to the nature of GLMM we were unable to calculate the p-value to accompany the results. Instead, we use a bootstrapping (boot.glm function) to calculate the CI. We see that subject's rates of pulled weight differed significantly from 0 (no difference in subject's response in relation to weight between different partners) (*X = 45.77,* CI [28.92, 63.12]) suggesting that they were moving significantly different amounts of weight when they were paired with different partners.

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

Model 8 investigated whether subjects' probability of the subject to pull was influenced by the partners' previous decisions to pull within a session. In this model we excluded the first trial of each session, as subjects had no previous experience before that trial. Therefore, we only used data were subjects had previous experience with a partner. As a response we used the ME index. We expected that the likelihood to pull would have been constant regardless of the partners' previous decisions to pull. However, in the extreme cases where the partners would have been very reliable, we would have expected subjects to pull less. We also expected the type of trial to influence subjects' likelihood to pull, pulling more often in short time trials in order to secure the rewards. The full model included the test variables, weight condition, type of trial, session, trial and phase as well as the interactions: type of trial, session, trial and previous experience each with weight condition. The control variables were: sex of the dyad, phase, type of trial, trial, session and the total time until the subjects touches the reward as fixed effect; subject and dyad as random effects and the random slopes (see Table A2). The comparison between the full and the null model was non-significant (GLMM: χ^2_8 = 6.202, *P* = 0.4, *N* = 1228) (see Table A9).

Model 9. Likelihood to wait before pulling (GLMM)

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

Table 1

Models conducted in the study (LMM: linear mixed model; GLMM: generalized linear mixed model. 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 91-8), 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.

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

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 91-8), 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

Table A3

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

Table A4

Table Model 2

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

Table A5

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

Table A6

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

Table A7

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

Table A8

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

Table A9

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

Table A10

Table Model 9

Test category	Estimate	Standard Error	CI (95%) of the full model
Intercept	3.822	0.756	2.648/5.673
Phase	0.075	-0.332	-0.332/0.507
Sex of dyad	NA	-	-
Weight condition*Type of trial	-0.552	0.514	-1.641/0.627
Weight condition*Trial number	-0.281	0.334	-1.108/0.361
Weight condition*session number	0.574	0.302	-0.013/1.239

Figure captions

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

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

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

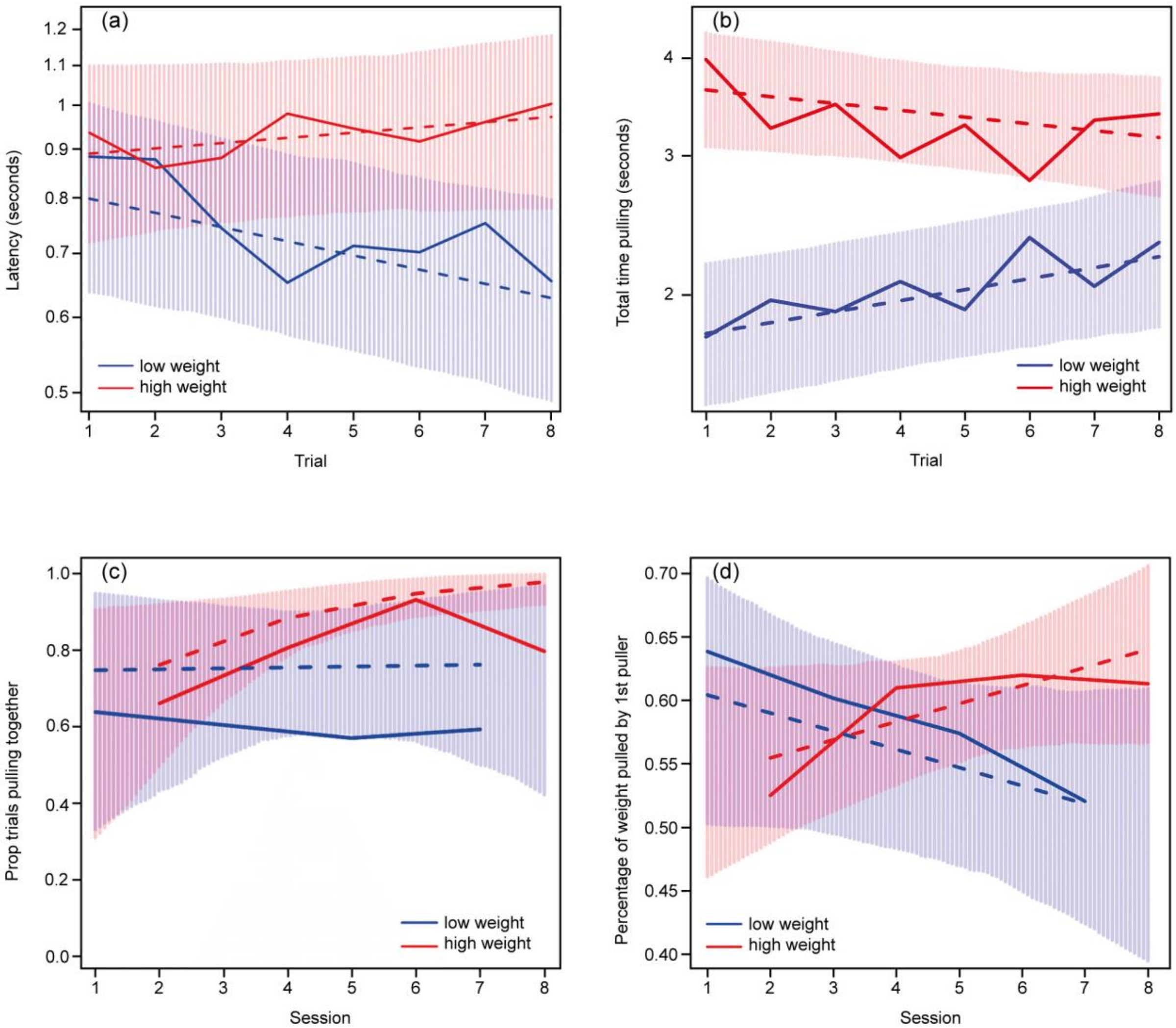
Figures A1 Apparatus characteristics

Figure A2 Apparatus characteristics

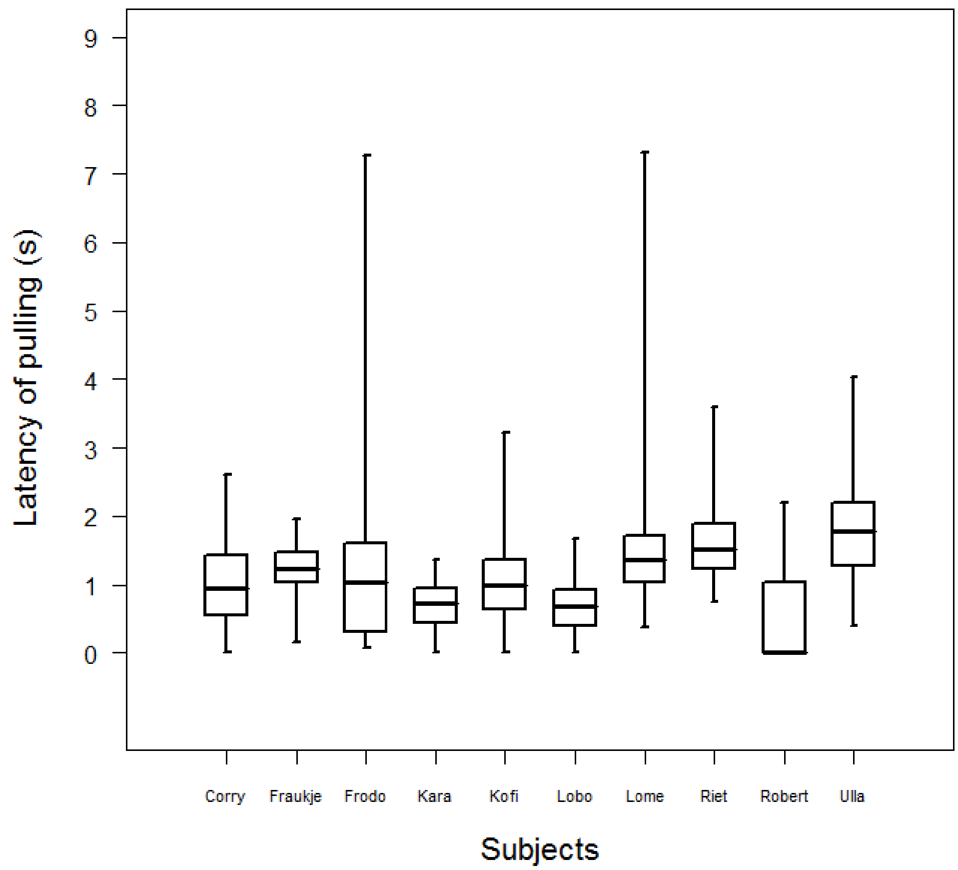
Figures

1

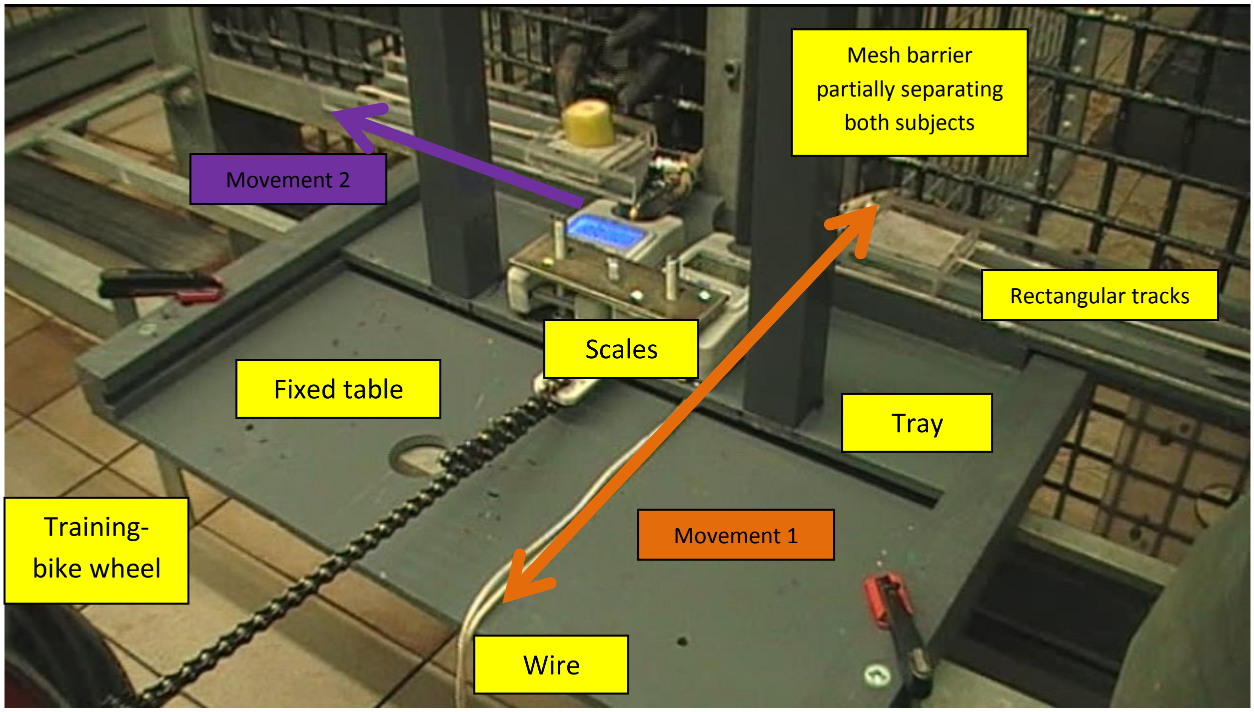
2


(a)
Latency (seconds)
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
low weight
high weight
1 2 3 4 5 6 7 8
Trial
(b)
Total time pulling (seconds)
4
3
2
low weight
high weight
1 2 3 4 5 6 7 8
Trial
(c)
Prop trials pulling together
1.0
0.8
0.6
0.4
0.2
0.0
low weight
high weight
1 2 3 4 5 6 7 8
Session
(d)
Percentage of weight pulled by 1st puller
0.70
0.65
0.60
0.55
0.50
0.45
0.40
low weight
high weight
1 2 3 4 5 6 7 8
Session

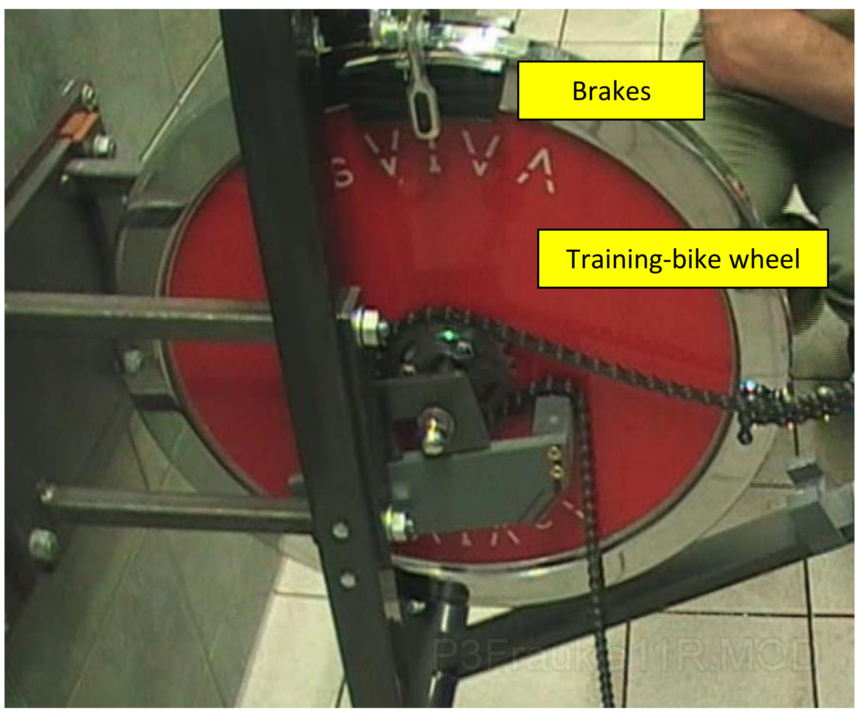
3


Latency of pulling (s)
0
1
2
3
4
5
6
7
8
9
Corry
Fraukje
Frodo
Kara
Kofi
Lobo
Lome
Riet
Robert
Ulla
Subjects

A1


Mesh barrier partially separating both subjects
Movement 2
Rectangular tracks
Scales
Fixed table
Tray
Training-bike wheel
Movement 1
Wire

A2


Brakes
Training-bike wheel