

# *COORDINATION IN CONFLICT SITUATIONS*

A COMPARATIVE INVESTIGATION OF THE COORDINATION STRATEGIES  
THAT CHILDREN, CHIMPANZEES AND BONOBOBOS  
USE TO SOLVE SITUATIONS OF CONFLICT

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M.Sc Alejandro Sánchez Amaro

geboren am 06.01.1988 in Sant Cugat del Vallès, España

Dekan: Prof. Dr. Erich Schröger

Gutachter: Prof. Dr. Michael Tomasello

Prof. Dr. Fernando Colmenares

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# INTRODUCTION

When thinking about cooperation we tend to inevitably envision acts of help, mutual effort or comfort directed toward others. As a matter of fact, cooperative acts constitute a fundamental part of our personal lives, and of human societies. We constantly interact with other people by joining efforts towards common goals such as when we play a football match, by asking for help when we get lost in an unknown place, by providing information when it is requested of us or even by joining in simpler cooperative endeavours such as talking or walking together. However, cooperation is a widespread behavioural strategy among animals other than humans; and for instance, great apes (henceforth apes) also need to cooperate with conspecifics to reap the benefits of their group living.

However, cooperation might entail a high-demanding endeavour for the individuals involved. This is especially true for socially complex animals such as humans and apes, living in ever-changing societies of different individuals having their own personalities, abilities, motivations and personal interests. In these species, individuals need to coordinate their actions effectively to achieve cooperative goals, especially when those require of simultaneous action. Moreover, individuals in these species are likely to face conflicts of interest when they need to decide whether or not to cooperate with other group members. During cooperative hunts, for instance, some chimpanzees may invest less by waiting for other group members to initiate the chase and, despite not participating themselves, still manage to obtain a piece of meat after the hunt has finished. However, if no chimpanzee starts hunting, no one would benefit. Humans also need to manage situations in which people have different interests but, ultimately, all of them prefer to reach a compromise to resolve the conflict. Examples of these situations are present in our everyday life: although mutually sharing the efforts would be the best strategy for a group of friends when they meet to prepare a barbeque or for colleagues to write a manuscript, free-riders are always ready to avoid the costs and benefit from the derived payoff. Yet, in those situations individuals are still better off if they keep cooperating than if they do stop: if everybody prefers another to cook or to write there will be no steak to eat and no paper to publish. Importantly, besides the conflict of interest inherent to any cooperative situation, individuals usually have more than one course of action available, increasing the coordination challenge. For instance, they can mutually cooperate by acting together, take-turns over the collaborative endeavour, pursue the goal on their own or free-ride with the hope that others will carry out the work.

Although natural observations suggest that humans and other apes may have complex strategies for solving coordination problems, controlled experiments are essential to determine which strategies they are employing. Therefore, in light of the increasing evidence of the complexity of the problems that these species face, new experimental paradigms that account for that complexity are particularly necessary. These paradigms will need to confront individuals with more complex situations for coordination where multiple solutions are available by combining the need for cooperation with the necessity to manage conflicts of interest between individuals.

In this thesis I will therefore investigate how humans and apes coordinate their actions and take decisions to strategically manage situations of conflict resembling natural scenarios for cooperation. To do so, I will present pairs of children, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), our two closest living relatives, with different tasks adapted from behavioural game theory, which vary in the degree of coordination required as well as in the nature of the risks associated with subjects' decisions. Comparing humans with our closest living relatives in these contexts will allow me to shed light on the cognitive processes underlying both children and apes' decision-making strategies to coordinate, and ultimately, to further understand the uniqueness of human cooperation.

## *1.1 Theoretical background*

Cooperation, the ability and motivation of individuals to perform costly actions in order to achieve goals not available otherwise is an important part of social animals' life (Dugatkin, 1997). Although cooperative patterns are everywhere —from unicellular organisms to human societies (Maynard Smith & Szathmary, 1997), cooperation is theoretically hard to explain. In populations composed of cooperators and defectors, the later will always have an advantage: they will avoid cooperative costs while benefitting from cooperators' investments. Evolutionary theory will therefore predict cooperators to become extinct across generations (Dawkins, 1976). This problem is circumvented among genetically related individuals. Hamilton's inclusive fitness theory states that, by sharing the same genes, genetically related individuals can obtain indirect fitness benefits from being altruistic to each other (Hamilton, 1964; West, El Mouden & Gardner, 2011). This is elegantly encapsulated in the Hamilton's rule: a cooperative behaviour will be stable as long as the benefits conferred to the receiver multiplied by the coefficient of relatedness between the receiver and the actor will out-perform the costs paid by the actor. Among unrelated individuals the coefficient of relatedness tends to be close to zero. Consequently, cooperative acts among non-kin should not thrive.

However, cooperation among unrelated individuals has evolved. To explain this phenomenon, several hypotheses have been postulated (Nowak, 2006; Trivers, 1971; West, Griffin & Gardner, 2007; Wilson & Sober, 1994). Yet, for the explanatory purpose of this work, I will focus on cooperative acts conducted by one individual (unilateral cooperation) and cooperative acts in which more than one individual contribute simultaneously (mutualistic cooperation or collaboration).

### *Unilateral cooperation*

When an individual acts at a cost for itself in order to benefit another one, we say that the former is acting altruistically. Unilateral acts of cooperation should not be stable in nature (unless the recipient of the altruistic act is sufficiently genetically related). Altruistic individuals should be out-performed by those who do not pay the costs of cooperation and thus have lower probabilities to survive and reproduce. However, this picture radically changes if individuals engage in reciprocal altruistic acts across time (Trivers, 1971). The rationale of reciprocal altruism (often referred as direct reciprocity) is apparently simple: an actor performs a costly behaviour in favour of a recipient, and the recipient reciprocates in the future. For the actor the immediate benefit of defection is thus out weighted by the future benefit that accrues from the recipients' behaviour.

Although reciprocal altruism has been considered one of the main mechanisms to explain the emergence of cooperation between non-related individuals (Nowak, 2006), it suffers from several drawbacks. First, it presupposes that organisms possess the cognitive skills to successfully reciprocate across time, including a capacity for individual recognition (Stevens, Cushman & Hauser, 2005; Trivers, 1971), the ability to remember their cooperative partner together with the value of the reciprocated reward (Stevens et al., 2005; Stevens & Hauser, 2004 but see Schino & Aureli, 2009 on emotional bookkeeping) and the capacity to delay immediate outcomes in favour of greater benefits in the future (Milinski & Wedekind, 1998; Stevens & Hauser, 2004). In fact, clear examples of reciprocal patterns in nature are scant (Clutton-Brock, 2009; Hammerstein, 2003; West et al., 2007; but see Raihani & Bshary, 2011).

Second, reciprocal altruism assumes that individuals engage in dyadic interactions, based on a process of partner control in which cooperation between isolated dyads is maintained by sanctioning partners' defective behaviour and rewarding cooperation (Schino & Aureli, 2016; Trivers, 1971). However, in nature, individuals usually have the possibility to interact with multiple partners. Although they can

avoid defecting partners by choosing the partners with whom they interact<sup>1</sup> (Noë & Hammerstein, 1994), the delay between the cooperative act and the benefit still gives individuals the possibility to defect (i.e., one individual can defect and change its partner to defect again; Gilby, 2012).

Contrary to the limited evidence of reciprocity in non-human animals, reciprocal altruism appears to be common in humans and probably played an important role in the evolution of human cooperation (Bowles & Gintis, 2001; Palameta & Brown, 1999; Rand & Nowak, 2013; Trivers, 1971; West et al., 2011). Different hypotheses have been developed stemming from the premise that humans reciprocate altruistic acts.

According to the Mismatch hypothesis (Burnham & Johnson, 2005), altruism towards unrelated individuals would be a maladaptive consequence of previous adaptations for living in ancestral societies characterized by high degrees of genetic relatedness and small numbers of individuals, which allowed for repeated interactions and, fostered opportunities to cooperate between highly related group members.

Other authors have proposed the concept of indirect reciprocity to explain the emergence of cooperation among non-kin over long periods of time. This mechanism relies on the actors' capacity to choose partners based on their reputation (i.e., based on their past cooperative or defective behaviour toward all group members), rather than on the personal history of previous interactions between actor and partner (Alexander, 1979; Leimar & Hammerstein, 2001; Milinski, Semmann & Krambeck, 2002; Nowak & Sigmund, 2005).

Alternatively, other accounts suggest that kin-based or reciprocity accounts alone cannot explain the emergence of large-scale human cooperation. At some point in our evolutionary history, reciprocal altruists became "strong-reciprocators" who paid the costs of cooperation and punished others that did not cooperate (Bowles & Gintis, 2003, 2011; Gintis, 2000) (these social preferences could appear *de novo* as result of small behavioural modifications). These new social motivations to cooperate likely fostered new ways to interact with individuals who belonged to the same social networks, giving rise to groups sharing cultural practices and norms of behaviour transmitted between generations via learning and imitation, through a culture-gene co-evolutionary process (Boyd & Richerson, 1988; Chudek & Henrich, 2011; Chudek, Zhao & Henrich, 2013; Mesoudi, 2009). As a consequence of these intricate patterns of learning (Chudek, Heller, Birch & Henrich, 2012; Henrich & Gil-White, 2001), groups creating social norms that fostered reciprocation (i.e., binding expectations about how people

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<sup>1</sup> Individuals are not completely "free" to choose their partners. In nature, factors such as dominance rank or social organization constraint individuals' possibilities to choose among social and mating partners (Kutsukake & Nunn, 2006; Seyfarth, 1977).

should behave in cooperative contexts) became more successful and spread (e.g., Diamond, 1997; Soltis, Boyd & Richerson, 1995), outcompeting less cooperative groups through a process of cultural group selection (Chudek & Heinrich, 2011; Henrich, 2004; Richerson, et al., 2016).

Finally, an interesting alternative to explain the emergence of cooperation among unrelated individuals through reciprocity, suggests that reciprocal acts among non-kin are easier to explain if we assume that each group member has stakes in other conspecifics (the Stakeholder model; Roberts, 2005). Individuals may therefore become interdependent regardless of previous reciprocal patterns of interactions, as a by-product of the needs of group living (e.g., reducing predation risks through increased vigilance). Either way, as they are interdependent, they have to care about each other's welfare and so, the temptation to defect is minimised.

### *Mutualistic collaboration*

The notion of interdependence entails a need to interact with another individual in an obligate form. Some species often need to collaborate to obtain simultaneous benefits that cannot be achieved otherwise, and therefore, defection becomes a less attractive option. This form of cooperation, known as mutualistic collaboration is widespread in nature (Boucher, 1988, Clutton-Brock, 2009; Connor, 1986). From an ultimate perspective a mutualistic act provides a simple explanation for the evolution of cooperation as the immediate benefits obtained by all individuals significantly diminish the incentive to free-ride. During mutualistic cooperation, individuals' best option is thus to cooperate in their own self-interest (Völter, Rossano & Call, 2015). However, from a proximate perspective effective mutualistic collaboration might not be as simple as it seems. Animals, for instance, need to coordinate their actions in space and time. In some species, coordination can be explained by the use of very simple behavioural rules and associative learning mechanisms operating at the individual level in relation to local parameters like speed and position of individuals (Bailey, Myatt & Wilson, 2013; Couzin & Krause, 2003). For instance, fish schools or bird flocks are examples of self-organization among vertebrates (Hildenbrant, Carere & Hemelrijk, 2010; Ward, Sumpter, Couzin, Hart & Krause, 2008). In some cases, also primates, including humans, might coordinate their decisions based on pre-programmed sets of actions and heuristics (Dyer, Johansson, Helbing, Couzin & Krause, 2009; Petit & Bon, 2010; Strandburg-Peshkin, Farine, Couzin & Crofoot, 2015). However, in other occasions, primates are capable of coordinating decisions and actions in more complex and flexible ways, in a process of strategic decision-making. This ability might have evolved as a response to adaptive pressures such as the need to forage on unevenly distributed food resources (Milton & May, 1976)

and to interact with unpredictable social partners (Byrne, 1994; Dunbar, 1998). This would have led primates to evolve enhanced cognitive adaptations such as behavioural flexibility and a capacity to form mental representations which might be especially useful when it comes to coordination.

Yet, despite its pervasiveness across the animal kingdom, mutualism has received little attention in some animal taxa such as primates (Gilby, 2012). Recently, mutualistic collaboration has been proposed to have played a central role in the evolution of human cooperation (Sterelny 2012, 2016; Tomasello, Melis, Tennie, Wyman & Herrmann, 2012). According to the Interdependence hypothesis (Tomasello et al., 2012), at some point in our evolutionary history, ancient hominids were forced to collaborate for mutual benefit in order to survive —for instance, to hunt large prey not otherwise attainable. This first key step in the evolution of human cooperation strengthened individuals interdependencies while fostering tolerance between them to overcome coordination challenges. As a consequence, unilateral cooperative acts such as helping and comfort would no longer constitute an evolutionary puzzle, as mutualistic partners would have felt obliged to care about each other for their mutual success (in a manner similar to the Stakeholder model described above). Over time, more efficient collaborators passed their genes across generations, while free-riders faded away. This selective pressure led to the formation of bigger human groups, in which cultural practices and norms gave rise to more complex forms of cooperation, serving as a starting point for the evolution of modern humans' unique forms of cognition and morality.

### *Conflicts of interest*

Cooperation can be thus maintained in nature through collaborations or reciprocal interactions among individuals. However, in spite of its prevalence in nature, cooperative acts are always intertwined with the temptation to defect, triggering inevitable conflicts of interest between cooperators, which need to be solved for cooperation to occur.

In the case of reciprocity, the temptations to defect are evident: individuals may reap the benefits from their partners help without reciprocating in return. In human societies, several mechanisms have evolved to reduce defections. Reputational concerns, for instance, tend to prevent people from free-riding (Bateson, Nettle & Roberts, 2006; Wedekind & Milinski, 2000) and third-party individuals are usually willing to sanction free-riders even at a personal cost (Fehr & Fischbacher, 2003), despite decreasing their fitness in relation to others unwilling to sanction (second order free-riders; Heckathorn, 1989; but see Panchanathan & Boyd, 2004). In the case of mutualisms, individual



motivations to defect are alleviated due to a shared interest to reap mutual benefits. Moreover, in contrast to reciprocity, this form of cooperation does not pose problems such as time discounting or the uncertainty of future interactions (Sterelny, 2016). Yet, unequitable reward distributions (i.e., distributions in which resources are not divided equally or according to individual efforts) may still give rise to a conflict of interest between collaborators.

In nature, common scenarios that test the coordinative abilities of individuals to cooperate together against their temptation to defect are *collective action problem* (CAP) (Heinsohn & Packer, 1995; Nunn, 2000; Nunn & Lewis, 2001; Willems, Hellriegel & van Schaik, 2013). A CAP can be understood as a situation resulting from the need for public good which is costly for individuals to garner, but benefits the whole group including individuals who do not contribute to the good (Nunn & Lewis, 2001). In a prototypical CAP, whilst collaboration towards a common goal is the most efficient strategy for the group as it results in shared benefits otherwise unattainable, the most efficient strategy from an individual perspective is to avoid the costs of cooperation while still benefiting from it. Yet, if all individuals defect, nobody will benefit. Interestingly, these scenarios are also unique in the sense that individuals not only have to decide whether to cooperate or defect, but also the way in which they can achieve cooperation. For instance, in a situation of cooperative hunting (Gilby, Eberly & Wrangham, 2008), individuals can mutually collaborate, increasing the likelihood of a successful hunt or chase alone and reciprocate in the future.

In the case of non-human animals, some accounts suggest that CAPs can be solved either through majority consensus or by the decisions of a leader, which is usually a dominant group member (Conradt & Roper, 2005; King & Sueur 2011; Sumpter & Pratt, 2009). Examples of CAPs among non-human animals can be found when group members need to decide among different travel routes (Ruckstuhl, 1998; Strandburg-Peshkin et al., 2015) or during group and territorial defence (Kitchen & Beehner, 2007; Nunn, 2000). In all these situations, individuals may have opposite preferences (e.g., where to move next) or may prefer to take advantage of others' actions (e.g., to avoid defensive costs). However, it is in their common interest to remain within the group and maintain its integrity as it provides benefits such as defence against predators or the possibility to find mates (Krause & Ruxton, 2002). In humans, economic models have been designed to understand how human societies overcome CAPs (Hardin, 1968; Olson, 1965; Ostrom, 1990). Recent models, for instance, suggest that individuals in a leadership position, with higher stakes or for whom the contribution costs into a CAP are lower, will contribute more in overcoming CAP, sometimes ending up with a smaller payoff than the rest of group members (Gavrilets, 2015; Gavrilets & Fortunato, 2014). Experimental research has found that at a local level, communities have reached successful solutions to overcome CAP involving common-pool resources through the creation of self-managed arrangements among locals (e.g.,

fishermen taking turns to fish in their favourite spot; Berkes, 1986; Ostrom, 1990; but see Ostrom, Burger, Field, Norgaard & Policansky, 1999 for global level challenges). Moreover, according to recent models, leadership helps to solve CAP in small-scale societies (Glowacki & von Rueden, 2015).

However, the study of CAPs has mainly focused on group level decisions, especially among non-human animals, without considering the motivations and the cognitive mechanisms underlying individuals' decision-making strategies in these situations. In the present dissertation, I explore humans' abilities to solve conflicts of interest in these types of cooperative situations from a dyadic perspective, and in order to obtain a broader view, I compared them with our closest living relatives, chimpanzees and bonobos. Apes provide an ideal model to understand the evolution of human cognitive abilities, and the comparison of their behaviour with that of children in similar contexts can offer key insights into the proximate mechanisms that regulate individuals' decisions and actions in these contexts as well as their evolutionary roots, and in particular, how humans and apes coordinate when facing a conflict of interest.

For this reason, I confront pairs of children, chimpanzees and bonobos with situations that a) varied in the degree of conflict between participants and b) differed in the way subjects could coordinate their actions in order to reap the rewards, (i.e., together or unilaterally).

## *1.2 Human cooperation in conflict situations*

Humans are ultra-social animals, cooperating in many diverse ways and with a frequency uncommon to other species (Tomasello, 2014). We act altruistically even in some anonymous contexts (Eckel & Grossman, 1996, Gächter & Falk, 2002; although see Levitt & List, 2007), divide the outcomes of our collaborative efforts with others (Hill & Hurtado, 2009; Marlowe, 2005), punish unfair actions at a cost for ourselves (Cameron, 1999; Fehr & Fischbacher, 2003; but see Henrich, Heine & Norenzayan, 2010 for variations between different cultural groups) and coordinate in complex collaborative activities such as group hunting (Alvard & Nolin, 2002; Hill, 2002). In fact, we constantly need to coordinate our actions with others to succeed in our everyday interactions.

Thus, our success as a species appears to be linked to our special ways to cooperate with others (Bowles & Gintis, 2011; Tomasello, 2009). These exceptional human abilities and motivations to cooperate are grounded in unique cognitive skills such as the ability to share intentions and goals, to engage in joint actions for common objectives and to recognize the interrelation of different

individuals participating in cooperative endeavours (Call, 2009; Carpenter, 2009; Tomasello, Carpenter, Call, Behne & Moll, 2005). In other words, from early on in our development we are already equipped with the psychological abilities and motivations for shared intentionality, the “ability and motivation to engage in collaborative activities with others through the creation of joint goals” (Tomasello et al., 2005).

From a very young age, infants engage in cooperative behaviours such as helping (Liszkowski, Carpenter, Striano & Tomasello, 2006) and sharing (Brownell, Iesue, Nichols & Svetlova, 2013; Brownell, Svetlova & Nichols, 2009). By the age of 20-24 months old, toddlers are capable of coordinating simple movements to coordinate with their cooperative partners (Eckerman, Davis & Didow, 1989). By the age of two, they are already capable of actively coordinating their actions with peers to reach common goals (Brownell, Ramani, Zerwas, 2006) and to solve simple problems collaboratively (Ashley & Tomasello 1998; Brownell & Carriger, 1990). Later, between ages three to five, children begin to understand the normative side of their collaborative activities, feeling committed to the joint goals shared with their peers (Hamann, Warneken, Greenberg & Tomasello, 2011) to the point that they attempt to re-engage their partners into ongoing joint tasks if those partners attempt to leave (Warneken, Gräfenhain & Tomasello, 2012). At the same age, children are capable of solving collaborative tasks by taking into account the different roles that partners must adopt to solve a joint task (Fletcher, Warneken & Tomasello, 2012). They are also able to plan division of labour in collaborative tasks (Warneken, Steinwender, Hamann & Tomasello, 2014). From three year old, children also start to reciprocate in cooperative tasks (Warneken & Tomasello, 2013). For instance, they share more with partners who have previously shared with them or with others (Levitt, Weber, Clark & McDonnell, 1985; Olson & Spelke, 2008; Warneken & Tomasello, 2013) and from 5-year old they are capable to match their partners’ previous actions (House, Henrich, Sarnecka & Silk, 2013) and to share more with a partner that could share with them in the future compared to a partner that was unable to reciprocate (Sebastián-Enesco & Warneken, 2015).

Children not only coordinate their actions in collaborative situations, but from a very young age they also coordinate their decisions to collaborate in efficient ways (Wyman, Rakoczy & Tomasello, 2013). Moreover, by the age of four, children are capable to leave aside a less preferred but secure reward to obtain a mutually preferred one (Duguid, Wyman, Bullinger, Herfurth-Majstorovic & Tomasello, 2014). In particular, when children shared visual contact they succeed with minimal communication (similar to chimpanzees in the same context). However, in the absence of visual contact, children used communication to establish mutual knowledge of the presence of the preferred reward, reducing the coordination failure. Furthermore, at the age of five they can use first (i.e., I know that I X) and second

order (i.e., I know that you know that I X) degrees of intentionality when they need to coordinate their actions with an absent partner (Grueneisen, Wyman & Tomasello, 2015).

Overall, these studies suggest that children from a very young age possess the capacities and intrinsic motivations to mutually coordinate their actions towards joint goals with their conspecifics, to provide help and to actively share resources. Later on in ontogeny, mechanisms for direct and indirect reciprocity develop to mediate acts of sharing (Olson & Spelke, 2008; Warneken & Tomasello 2013). As of yet, most research has focused on children's abilities to coordinate their actions in circumstances of mutual benefit, when they share the same goals and their interests do not compete (Duguid et al., 2014; Grueneisen et al., 2015 for examples). In these contexts, children share their mutual knowledge that a) each child is needed to successfully cooperate and b) that reaching the mutual goal is the best option for both (Bratman, 1992; Lewis, 1969; Schelling, 1960). Thus, from a theoretical point of view, children's intrinsic motivations should be very similar, as they share a strong preference for the same mutual goal. However, in some human cooperative interactions, individuals also have opportunities to free-ride (despite sharing a preference for a mutual goal), creating a conflict of interest between cooperative partners. In those situations, despite people's abilities to reciprocate their actions or collaborate simultaneously, each person would prefer to maximize their own outcomes by free-riding, resulting in a clear conflict between individuals when they need to actively coordinate.

Adults are capable of managing this kind of social conflicts in diverse ways. Firstly, when recurrent conflict interactions occur at a local level (i.e., with familiar or well-known individuals), people directly negotiate compromises to resolve them. Examples of these may include the division of family duties (one cleans the dishes while the other cleans the bathroom) or the establishment of mutual commitments to resolve conflicts of interest. One intuitive way to resolve this type of conflict is to take turns in the execution of a specific, sometimes costly, action (Helbing, Schönhof, Stark & Hołyst, 2005; Nowak & Sigmund, 1994). For instance, soldiers take turns to occupy the most dangerous positions during combats (Rominger & James, 2003). In this way, individuals can share the costs of their actions equitably.

However, little is known about children's capacities to coordinate when their interests compete, as well as the strategies they use to negotiate in those situations. Only recently, researchers have started to focus on these questions. In a recent study, for instance, Grueneisen and Tomasello (2016) presented 5-year old children with a version of the chicken game. In this task, each child had the option to cooperate or not with his or her partner. The optimal solution from an individual perspective would have been to defect while the partner cooperates. However, mutual defection resulted in no rewards. Alternatively, they could coordinate their actions by taking turns while losing part of their reward to

avoid mutual defection. In this task, children demonstrated that they could coordinate their actions by taking turns and they rarely failed to obtain the rewards. Moreover they used communicative acts to facilitate turn-taking interactions. In line with these findings, Melis and colleagues (Melis, Grocke, Kalbitz & Tomasello, 2016) presented pairs of 5-year old children with a collaborative task in which one child at a time could get rewards after both had collaborated. Children spontaneously took turns to obtain the rewards, in line with previous studies showing that children re-distributed unequal distributions after they had collaborated (Hamann et al., 2011; Warneken et al., 2014). In all, these studies show that from a very young age, children successfully manage conflict situations even when their interests are not aligned. Yet, little is known about children's performance in situations where they can decide whether to act together or alone to resolve their dispute and obtain mutual rewards<sup>2</sup>. Moreover, no study has so far investigated the evolutionary roots of coordination in this type of conflict situations from a comparative perspective.

### *1.3 Great apes coordination in conflict situations*

#### *Field experiments*

Chimpanzees and bonobos are social primates. Both species have a classic fission-fusion organization, living in multimale-multifemale groups with stable memberships, although community members form temporal subgroups (parties) that lack fixed composition. As a result of their social organization, these species need to maintain multiple relationships with kin and non-kin individuals (Marchant & Nishida, 1996; Watts, 2012). Although much of chimpanzees' and to a lesser extent bonobos social lives are governed by competition (Muller & Mitani, 2005), these species also engage in a variety of cooperative activities with conspecifics, including food sharing (Wittig, Crockford, Deschner, Langergraber, Ziegler, Zuberbühler, 2014; Yamamoto, 2015) and grooming (Goodall, 1986; Kano, 1989). Chimpanzees and bonobos also form mutualistic coalitions with other group members. For instance, male chimpanzees join forces to outperform other males from privileged positions (Watts, 1998) while female bonobos form coalitions to counteract male harassment (Tokuyama & Furuichi, 2016). Moreover, there is anecdotal evidence of altruistic acts in chimpanzees such as the case of an adult male chimpanzee

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<sup>2</sup> Notice that in previous studies children could not act together (Gruneisen & Tomasello, 2016) or could only act together for unilateral benefit (Melis et al., 2016), but could not resolve conflicts of interest via mutual collaboration (with the possibility to act on their own) for mutual benefits.

taking care of an orphan infant in the Tai Forest (Boesch, Bole, Eckhardt & Boesch, 2010). In other occasions, chimpanzees also need to coordinate in complex situations in which individual and group interests may conflict, for instance during group patrolling of territorial borders and cooperative hunts.

### *Group patrols*

Group patrols consist of several individuals travelling around the boundaries of their territory to protect it from out-group individuals (Watts & Mitani, 2001), and sometimes into the territory of neighbouring groups (Boesch, 2003; Wrangham, 1999). While this behaviour is very common among chimpanzees (Boesch, Crockford, Herbinger, Wittig, Moebius & Normand, 2008; Watts & Mitani, 2001; Watts, Muller, Amsler, Mbabazi & Mitani, 2006; Wilson, Wallauer & Pusey, 2004), it has not been reported in any bonobo community (Furuichi, 2011; Hohmann, 2001). Patrol bordering increases the probabilities to meet other groups, and thus may lead to inter-group aggressive encounters (Wilson, Hauser & Wrangham, 2001). As a consequence, chimpanzees can maximize their individual benefits by delaying their movements or letting others occupy the front positions of the patrolling party. To date, it remains unclear how chimpanzees overcome this CAP, and which individuals initiate these patrols and occupy the riskiest positions. While some studies have found that there might be specific individuals who are willing to start patrolling (Gilby, Wilson & Pusey, 2013), others have suggested that travel initiations by male chimpanzees positively correlate with mating success (Watts & Mitani, 2001) suggesting that those males who are more likely to benefit from the patrols —expanding their home range or increasing the number of females in the group— are also more likely to pay the associated costs with group patrols, including a tendency to go further compared to low ranking males when they visited the periphery of their range (Wilson, Kahlenberg, Wells & Wrangham, 2012).

### *Cooperative hunts*

Chimpanzees and bonobos hunt in groups although reports of cooperative hunts in bonobos are scant (Surbeck & Hohmann, 2008). Conversely, chimpanzee group hunts have been widely studied in several chimpanzee communities (Uehara, 1997). Demographic and ecological conditions vary across communities (Caldecott & Kapos, 2005; Inskipp, 2005) and these differences appear to impact communities' diverse hunting strategies (Boesch, 1994a; Newton-Fisher, 2015; Pruettz, Bertolani, Ontl, Lindshield, Shelley & Wessling, 2015). For instance, chimpanzees in Gombe seem to hunt in parallel with little if any coordination between them. In these environments chimpanzees do not probably

need to coordinate their actions in complex ways as they can constantly track their prey and other group members due to the short canopy of the forest (Boesch, 1994a). In contrast, the dense canopy in the Taï forest would hinder chimpanzees' visual access to their prey and group mates. Thus, to cope with the environmental contingencies, chimpanzees in Tai would have developed more efficient ways to coordinate their actions while hunting (Boesch, 1994a, 1994b, 2002).

Two main accounts have been proposed to describe the complexity of cooperative hunts in chimpanzees. One account suggests that each individual has a specific role during the hunt and it is also aware of each other's role and position (Boesch, 2002). Similarly to individuals acting as a team (Anderson & Franks, 2001), chimpanzees would therefore be able to effectively coordinate their actions towards the shared common goal. This explanation presupposes that chimpanzees have the ability to form joint goals and take complementary roles during hunts (Boesch, 2005) —skills that have so far only been detected in humans. A more parsimonious account therefore suggests that chimpanzees act in a "I-mode group behaviour" while hunting, in which coordination arises as the by-product of each individual trying to capture the prey on its own, while taking advantage of others' movements (Kun, Boza & Scheuring, 2006; Gilby & Connor, 2010; Tomasello et al., 2005; Tuomela, 2006) In this way, hunts are likely to be initiated by a single individual followed by other group members, resembling a Stackelberg or "leader-follower" strategy (von Stackelberg, 1934).

Regardless of the cognitive abilities required, cooperative hunting still posits a CAP, as hunts are a costly activity and individual chimpanzees might prefer others to start the hunt (Gilby & Connor, 2010). By waiting, chimpanzees can benefit in different ways: they can avoid the costs of the chase and they can also track the initial movements of the monkeys so they can act more effectively. However, the chances to get the prey increase and the group benefits from all individuals collaborating and sharing the prey. Moreover, the current interpretation of cooperative hunts as instances of CAP is supported by recent research suggesting that specific chimpanzees are more prone to pay the initial costs of the hunt and solve the CAP while promoting the likelihood that other members of the hunting party join in (Gilby, Machanda, Mjungu, Rosen, Muller, Pusey & Wrangham, 2015).

In the wild, it is clear that chimpanzees and bonobos are able to coordinate actions to cooperate in efficient ways even when dealing with complex scenarios. Yet, even though the observational study of natural behaviours such as cooperative hunts has been extremely useful to understand chimpanzees' and bonobos' coordinative patterns in real life scenarios, behavioural observations do not suffice to determine the exact decisions and strategies underlying individual actions in these contexts. For instance, in the case of cooperative hunts or group patrols, behavioural observations alone cannot provide any information as to whether initiators take into account others' decisions

before acting. Therefore, in order to address these questions in more detail, we need well-controlled methods which are more feasible to implement in experimental set-ups.

### *Experimental research*

As with children, the majority of experimental studies on apes' cooperation have mainly focused on the ability of pairs of chimpanzees to coordinate their actions towards common goals, in which collaboration is the only solution to solve the task and subjects' interests are completely aligned (Hirata & Fuwa, 2007; Melis, Hare & Tomasello, 2006a). In addition, some studies have also explored apes' capacity to reciprocate with conspecifics (Amici et al., 2014; Brosnan, Silk, Henrich, Mareno, Lambeth & Schapiro, 2009; Pelé, Dufour, Thierry & Call, 2009; Yamamoto & Tanaka, 2009) and overall have found that apes did not reciprocate in ways contingent to the partner's previous behaviour.

Focusing on mutual collaboration, early work demonstrated that pairs of chimpanzees succeeded when they had to pull together from a heavy box to obtain a reward (Crawford, 1937). Importantly, the box could not be moved by one individual alone so that apes needed each other to obtain the rewards. Although apes were able to coordinate their actions in these task and similar ones (Chalmeau, 1994; Chalmeau & Gallo, 1996), they may have achieved the goal by randomly pulling their ropes simultaneously, casting doubt on whether they really took into account their partners' actions to solve the task.

A better approach to the study of coordination presented pairs of chimpanzees with a long board baited at its ends. Importantly, only one rope was threaded through loopholes on the board, with each end within reach of one of the two subjects. Consequently, if only one chimpanzee pulled, the rope came loose without moving the platform, preventing chimpanzees from obtaining the rewards (Hirata & Fuwa, 2007; Melis et al., 2006a). In this task, chimpanzees were able to recruit the best collaborators based on previous experience (Melis et al., 2006a), by actively opening a door so that a partner could join them in the test room, and even waiting to pull the rope until the partner was ready to join in (Hirata & Fuwa, 2007). Moreover, in another related study, chimpanzees could solve a coordination problem by acting on different but complementary roles (Fletcher et al., 2012).

However, in these studies coordination might have been relatively easy to achieve as individuals were only presented with one option (i.e., pulling or not). Moreover, chimpanzees could have solved these tasks by simply waiting until some force is applied to the rope before pulling (see also Albiach-Serrano, 2015). Therefore, recent studies have focused on the abilities of chimpanzees to coordinate in more



complex situations in which individuals do not only need to coordinate their actions by performing a similar action at the same time, but also have to make similar decisions between different alternatives. To operationalize this situation, Bullinger and colleagues (Bullinger, Wyman, Melis & Tomasello, 2011a) presented pairs of chimpanzees with a Stag Hunt situation where each member of a pair had access to a less-preferred secure option (i.e., juice). However, after a certain time, they could coordinate their actions towards a mutually preferred option (i.e., pieces of banana), while losing access to the less preferred alternative. Therefore, chimpanzees experienced a coordination conflict, having to decide whether to abandon the secure reward, with the risk of losing all rewards if the partner does not coordinate. Importantly, in this task chimpanzees did not experience a conflict of interests as both individuals shared a mutual preference for the stag. Chimpanzees were capable to coordinate their actions towards the stag using a leader-follower strategy that consisted of the leader abandoning the less-preferred option to approach the stag, and the follower joining in right after. This strategy is in line with some accounts describing chimpanzees' group hunting behaviour in the wild (Gilby et al., 2015). In a follow up study Duguid and colleagues (2014) showed that when audible and visual cues were prevented, chimpanzees' success significantly decreased as compared to a full-view situation. However, chimpanzees still managed to coordinate their actions around half of the time, using a leader-follower strategy and occasionally communicating once they were next to the stag.

As yet, only few experimental studies have focused on how chimpanzees coordinate their actions to collaborate in situations with a real conflict of interest. In a first attempt, Melis and colleagues (Melis, Hare & Tomasello, 2009) presented pairs of chimpanzees with two identical baited trays. The first tray was equally baited on both ends while the second tray was unequally baited, providing more food to one of the subjects. This arrangement created a conflict of interest, as both chimpanzees preferred to pull from the side containing the highest amount of food. In this situation, subjects had to coordinate their pulling actions and also decide which tray to pull. Despite the apparent conflict of interest, chimpanzees succeeded in obtaining the reward in between 78-94% of the cases. However, when only one chimpanzee could obtain the resources from the collaborative work, cooperation tended to disintegrate over time (Melis et al., 2016). Therefore, as an overall result, these studies suggest that chimpanzees cooperate in mutualistic ways as long as both members of a pair obtain a net benefit from the interaction, even when the mutual benefit is unequally distributed. In contrast, when mutual efforts only yield benefits to one member of the party and members need to engage in reciprocal mechanisms to sustain cooperation, cooperation tends to disappear.

In a different line of research, Schneider and colleagues (Schneider, Melis & Tomasello, 2012) presented chimpanzees with more complex scenarios for cooperation in an attempt to mimic natural CAP situations. In this task, chimpanzee groups of three individuals were presented with a Volunteer's

Dilemma situation, in which a food dispenser released food in a main room as long as it was activated from an adjacent one. Importantly, from the adjacent room chimpanzees were not able to retrieve any reward. Thus, one chimpanzee had to volunteer by paying the costs of moving to the adjacent room and activate the mechanism while the others benefited from the food released. However, researchers found that the most dominant individual activated the dispenser and still obtained the majority of rewards, casting doubts on whether chimpanzees interpreted the task as a real CAP.

Contrary to chimpanzees, bonobos' abilities to coordinate in mutually collaborative set-ups have not been studied in such detail. When confronted with a task in which individuals needed each other to pull from a baited tray, Hare and colleagues (Hare, Melis, Woods, Hastings & Wrangham, 2007) found that bonobos succeeded as well as chimpanzees. Moreover, due to bonobos' higher rates of social tolerance towards conspecifics, unlike chimpanzees (Melis, Hare & Tomasello, 2006b), they were also capable to coordinate their actions and to pull together when they were confronted with monopolizable food (i.e., when the food was baited in the middle of the tray, equidistant to each individual). However, little is known about bonobos' abilities to collaborate and coordinate with others when their interests compete.

Yet, although these studies have explored different facets of individuals' abilities to coordinate and negotiate conflicts, other factors that are likely to influence individual decisions deserve some attention. First, in the majority of previous studies, chimpanzees had to collaborate to obtain the rewards facing no other alternatives to succeed (in Bullinger et al., 2011a and in Duguid et al., 2014 chimpanzees did not need to collaborate to obtain rewards but the collaborative option was the preferred for both individuals). In contrast, in more ecologically relevant scenarios such as when intergroup aggression arises, cooperative hunts start or patrol borders are initiated, individuals always face multiple options; for instance they can delay their actions to take advantage of others' movements, or they can act individually towards the achievement of the common goal, or do not act at all. Therefore, no work has yet explored the decision-making strategies that chimpanzees and bonobos would use in conflict scenarios in which collaboration is only one of the multiple options to solve the task.

Second, in natural scenarios such group hunting, individuals may face time constraints (e.g., prey availability) when having to decide whether to cooperate or not. Therefore, to explore the effect of time in chimpanzees and bonobos decision-making abilities when facing conflicts of interest, shorter time-frames are needed to increase the coordination challenges as well as the likelihood to fail.

Third, inter-individual differences in propensity to take risks are likely to influence in the decisions of chimpanzees and bonobos in these contexts. In general it has been suggested that bonobos are more

risk averse than their closest relatives, the chimpanzees possibly as a by-product of adaptations to different food resources (Haun, Nawroth & Call, 2011; Heilbronner, Rosati, Stevens, Hare & Hauser, 2008; Rosati & Hare, 2012). Nevertheless, these studies have focused on apes unilateral decisions in non-social scenarios or in scenarios confronting the subject with a human competitor (Rosati & Hare, 2012). In the case of humans, individuals tend to take riskier decisions when others observe them compared to when they are alone, a phenomenon called *risk shift* (Gardner & Steinberg, 2005; Vinokur, 1971). Thus, it is possible, that when chimpanzees and bonobos are confronted with social scenarios in which actors' and partners' decisions are interdependent, their propensities towards risky choices may differ, as compared to individual contexts.

Fourth, in chimpanzees' and bonobos' everyday life, conflicts of interest do not only occur when individuals need to coordinate to reap cooperative benefits. In competitive context, such as when two individuals want to mate with a third one, conflicts of interest are constantly present —although in this kind of situation coordination might not be necessary (i.e., when both individuals prefer to mate before the other one). Therefore, in the context of this thesis, one possibility to make sense of individuals' decisions and actions when their interests conflict in cooperative contexts is to present them with competitive situations in which every subject best strategy is to act on its own (i.e., pull from a tray to obtain most of the food before the partner). With this condition, we fulfill two goals: we present subjects with an ecologically relevant situation that serves us, at the same time, as a baseline to explain and compare our results.

Overall, in order to systematically compare apes' and children's strategies to coordinate, we would need to present these species with the same social dilemmas across different scenarios, differing in the degrees of conflict and risk associated. For this purpose, I will draw upon adapted models taken from the game theory literature.

## *1.4 Models of cooperation and conflict*

Game theory is the study of conflict and cooperation through mathematical modelling. A prototypical game consists of a 2x2 matrix that depicts each player's choices (X and Y in Figure 1) and payoff outcomes (A, B, C, D in Figure 1) as a result of their previous choices.

		Player 2	
		X	Y
Player 1	X	A	B
	Y	C	D

Figure 1. Prototypical payoff matrix of a dyadic game theory model.

According to Halevy and colleagues (Halevy, Chou & Murnighan, 2012), two general types of models can be used to understand humans' psychological mechanisms and motivations to coordinate their decisions and actions: cooperative and conflict models. On one hand, cooperative models such as the Stag Hunt (Skyrms, 2004) and the Maximizing game (Marwell, Ratcliff & Schmitt, 1969) present scenarios in which both agents share their preferences (Balliet, Tybur & van Lange, 2016). In a typical cooperative scenario, both agents obtain the highest benefits by cooperating. On the other hand, conflict models such as the Snowdrift game<sup>3</sup> (Sugden, 1986) and the Prisoner's Dilemma (Tucker, 1950; Rapoport & Chammah, 1965) present agents with situations in which their interests compete with each other, and individuals obtain the highest benefits by defecting while the partner cooperates.

In analytic terms, a crucial factor to compare these two sets of models resides in their Nash Equilibrium. The Nash Equilibrium is defined as the state of a game in which no player can benefit from a unilateral change of strategy (Nash, 1950). In cooperative games like the Stag Hunt, mutual cooperation is the best strategy for both players and it is also a Nash Equilibrium solution. In contrast, in conflict games such as the Snowdrift game and the Prisoner's Dilemma, mutual cooperation is not a stable strategy. In these games, although mutual cooperation provides more benefits than mutual defection, individuals would prefer to defect when their partners cooperate, originating a conflict of interests between players. However, there is a crucial difference between the two models. In the Snowdrift game, unilateral cooperation yields a benefit and thus, individuals would prefer to

<sup>3</sup> This game is also referred as the Chicken game (Rapoport & Chammah, 1966) or the Hawk-Dove game (Maynard Smith, 1978).

cooperate rather than defect given that the partner defects. However, in the Prisoner's Dilemma, unilateral cooperation is the worst outcome, and so, to avoid these high costs, players would end up defecting. In short, it is expected that individuals would show more cooperative behaviour in a Snowdrift situation as unilateral cooperation would be rewarding. Thus, for the purpose of this work, I will use an adapted version of the Snowdrift game and the Prisoner's Dilemma to model cooperative scenarios in which individuals' self-interests compete.

### *The Snowdrift game*

In the classic description of the Snowdrift scenario (Sudgen, 1986) 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. In this scenario, each driver should prefer the other to carry out the whole work. However, if one of them clearly defects, the other should shovel the snow and pay the whole burden to return home. Thus, on one hand both drivers have a common goal that can be achieved through mutual cooperation (cleaning the snow together) but on the other hand, as their interests are conflicting, they may prefer to wait for their partner to act alone and benefit from their cooperation without incurring any cost. However, if both remain in their car and free ride, they run the risk that none cooperates and both lose.

The Snowdrift models a situation in which the best strategy for an agent is to carry out the opposite action of its partner. Figure 2 depicts a prototypical Snowdrift payoff matrix. In this scenario, if player A chooses to cooperate, player B's best strategy is to defect and viceversa. Thus, the Snowdrift game can be thought of as an anti-coordination game with two stable strategies –the two anti-coordination outcomes. Yet, this analysis only exemplifies a singular Snowdrift interaction. Reality is much more complex and group living animals such as humans and apes are very likely to encounter situations in which the same individuals recurrently face similar conflicts. In those situations, individuals may develop other strategies to manage repeated sequences of conflict.

		Player 2	
		Cooperate	Defect
Player 1	Cooperate	<b>2,2</b>	<b>1,3</b>
	Defect	<b>3,1</b>	<b>0,0</b>

Figure 2. Snowdrift payoff matrix.

During repeated encounters, one possible way to overcome the conflict set-out by the Snowdrift game, for instance, is to collaborate and obtain mutual benefits while sharing the costs of cooperation. This, however, is not a stable strategy as at any given time one could defect and obtain most of the benefits if the partner cooperates. Another way to solve the dilemma is to take turns, or reciprocate, over the cooperative endeavour. In this way, individuals would benefit from the cooperative acts of their partners every second time while they would pay the costs of cooperation half of times. Thus, turn-taking is a stable strategy that resembles the Nash Equilibrium of the game. Yet, although both collaboration and turn-taking strategies may yield to the same benefits in the long term, only the latter is immune to defection by rational agents. Moreover, in a Snowdrift situation, individual differences may lead to stable fixed strategies where a dominant individual always defects while the submissive partner pays the recurrent costs of cooperation (Maynard Smith & Price, 1973).

According to recent literature, CAPs such as group hunting and other animal cooperative activities such as territorial defence or group foraging posit challenges that are similar to the Snowdrift game (reviewed in Kun et al., 2006; Doebeli & Hauert, 2005). From this perspective, CAPs can be understood as N-person Snowdrift dilemmas between group members. Other researchers have suggested that cooperation is more likely to evolve in Snowdrift-like scenarios as the majority of cooperative acts in nature lead to positive benefits for cooperators as opposed to scenarios in which unilateral cooperation leads to the worst outcome for the cooperator (Bshary, Zuberbühler & van Schaik, 2016). These theoretical accounts have been in turn supported by empirical results in human dyads (Duffy & Feltovich, 2002, 2006; Kümmerli, Colliard, Fietcher, Petitpiere, Russier & Keller et al., 2007;

Rapoport & Chammah, 1966) and groups (N-person games) (Liebrand, Wilke, Vogel & Wolters, 1986; Wit & Wilke 1992), and by agent-based simulations (Doebeli & Hauert, 2005; Doebeli, Hauert & Killingback, 2004). For instance, Duffy and Feltovich (2002, 2006) have shown that people tend to cooperate more when they are presented with a Snowdrift compared to a Prisoner's Dilemma situation. All together, these findings suggest that organisms may be more prone to cooperate in Snowdrift scenarios, due to the low risk of mutual defection and the fact that cooperative acts provide net benefits regardless of other individuals' actions. Therefore, the Snowdrift game stands out as a promising model to study decision-making strategies when individuals need to coordinate their actions in spite of a conflict of interest.

### *The Prisoner's Dilemma*

In the traditional version of the game, two suspects are interrogated in separate rooms. Each can either confess the crime, thereby implicating the other (defect), or keep silent and cooperate. If both remain silent, both get the same treatment, one year in prison. However, if one confesses while the other keeps the secret, the confessor is set free while the cooperator awaits for the worse sentence, three years in prison. Finally, if both confess, both face the same penalty, two years in prison, which is worse than if both had remained silent. Thus, no matter what the other suspect does, each can improve his own position by confessing.

Thus, the Prisoner's Dilemma models a situation in which an agent's best strategy is to always defect regardless of its partner's action –the Nash Equilibrium of the game. Figure 3 illustrates the traditional Prisoner's Dilemma payoff. In this figure, it can be seen that regardless of player' A's choice (either to cooperate or to defect), player B's best choice is always to defect; and that mutual cooperation provides higher benefits for both players compared to mutual defection. Therefore, when individuals are confronted with iterated versions of a Prisoner's Dilemma game, mutual defection is no longer the best solution although it is the only stable outcome of the game. Therefore, individuals during repeated encounters need to efficiently deal with the conflict.

		Player 2	
		Cooperate	Defect
Player 1	Cooperate	<b>2,2</b>	<b>0,3</b>
	Defect	<b>3,0</b>	<b>1,1</b>

Figure 3. Prisoner's Dilemma payoff matrix (following the example above).

One intuitive way to solve an iterated Prisoner's Dilemma is to cooperate if your partner has previously cooperated (i.e., Tit-for-Tat strategy; Axelrod, 1987; Axelrod & Hamilton, 1981). When decisions are concurrent, Tit-for-Tat results in iterated instances of mutual cooperation. However, when decisions are not concurrent, a Tit-for-Tat strategy can be practically understood as players taking turns to reciprocate their cooperative costs in every following round of the game. Yet, if the costs of cooperation outperform the benefits, a turn-taking mechanism will not be stable.

In all, the Prisoner's Dilemma is perhaps the most influential model to study cooperation (Hauert, 2013). Still, despite its prevalence in the cooperation literature, there are few examples of non-human animals interacting in ways resembling a Prisoner's Dilemma game (Clutton-Brock, 2009; Doebeli & Hauert, 2005; Kun et al., 2006). It is possible that due to the high risks that the Prisoner's Dilemma imposes to cooperators, scenarios resembling this game are less common in nature, where mutualisms and interdependencies between group living animals decrease the risks to act cooperatively. In humans, experimental studies have shown that people do not seem to follow rational strategies but rather tend to behave more cooperatively than theoretically predicted (Andreoni & Miller 1993; Sally, 1995), even when presented with one-shot versions of the game (Camerer, 2003; Engel & Rand, 2014; Kiyonari, Tanida & Yamagishi, 2000). In any case, the Prisoner's Dilemma offers an elegant framework to explore the strategic decision-making capacities of children and apes to cooperate in high risk scenarios, in which unilateral cooperation is strongly penalized, compared to more relaxed situations such as in the Snowdrift game.



## 1.5 Focus of the dissertation

This dissertation is divided into three chapters.

### *Chapter 1*

In the first chapter of the dissertation I explored whether pairs of chimpanzees possessed the abilities to cooperate when their interests were in conflict. To recreate a conflict scenario, I used the Snowdrift game. For this purpose, pairs of chimpanzees were presented with a situation in which they could either pull together (mutual cooperation or collaboration) from a weighted tray and share the cooperative costs, or pull alone –unilaterally paying the burden of cooperation. As in a Snowdrift situation, in this study chimpanzees also had the opportunity to free-ride and get the benefits from their partners' actions. Importantly, pairs had a limited amount of time to solve the dilemma before the food disappeared, resembling natural situations such as cooperative hunts in which monkeys may leave at any time.

The main interest of the study was to explore whether chimpanzees would behave strategic in the conflict scenario, by trying to maximize the food rewards while minimising costs (i.e., waiting longer to pull when cooperation costs increased). Moreover, I was also interested in the strategies that individuals would adopt to overcome the conflict situation (i.e., acting unilaterally or collaborating). Finally, I explored whether chimpanzees would change their strategies depending on the identity of their partners in an attempt to investigate whether they adjusted their behaviour to the contributions of others.

### *Chapter 2*

In the first part of the second chapter (Studies 2a and 2b), I used a modified version of the Snowdrift game to address whether pairs of bonobos, chimpanzees and children would coordinate their actions when they were presented with a conflict task in the form of a rotatory tray baited with an unequal reward distribution. In the critical condition, the preferred reward could only be obtained by waiting for the partner to pull. This condition was compared to a *competitive* control in which the preferred reward could only be accessed by pulling before the partner. In both conditions, pairs had a limited amount of time to retrieve the rewards from the tray before those were removed. Contrary to the traditional Snowdrift game presented in the previous section, in this version mutual cooperation

within a trial was not possible but individuals could use other strategies over the course of the study to overcome the conflict of interest presented (e.g., through turn-taking).

The main interest of this second study was to explore whether chimpanzees, bonobos and children would behave strategic in this version of the Snowdrift, showing higher latencies to pull in Snowdrift trials compared to the *competitive* control condition. I was also interested in the strategies that the three species would use to coordinate their decisions and to maximize their reward. Finally, I investigated the role of communication when pairs of individuals needed to coordinate their actions to overcome situations of conflict.

Due to the strategies shown by some apes in the first section of this chapter, I tested pairs of chimpanzees and bonobos in a follow-up study (Study 3) to explore in more detail apes decision-making strategies when individuals' interests compete. In the second part of this chapter, I presented apes with the same apparatus we used in Study 2a with the addition of an alternative secure option for each individual. In this situation, each subject should decide whether to access the rotatory tray (social option) or the alternative option, which varied in the quantity of rewards presented between sessions (non-social option). From a rational perspective, apes had to access either the social or the non-social option depending on the rewards distribution and their partners' actions.

I hypothesized that the addition of an alternative option would allow subjects to better manage the risk and to behave more strategically compared to the previous study. With the opportunity to decide between different options we approximate ecologically relevant scenarios such as cooperative hunts. I expect subjects to take decisions based on the available options and their partners' likely decisions.

### Chapter 3

In the third and last chapter of the dissertation, I used the Prisoner's Dilemma model to further investigate the strategic capacities of chimpanzees and children to coordinate their actions in situations of conflict in which unilateral acts of cooperation resulted in the loss of all rewards for cooperators. The Prisoner's Dilemma was presented in the form of an elevator that either delivered all the rewards to a partner or to one-self. In the critical condition, the rewards could only be obtained by waiting for the partner to act first. In contrast, in the *competitive* control condition, the rewards could only be obtained by acting before the partner. Moreover, in this task subjects could also collaborate and divide the rewards by acting together at the same time in both conditions. As in the previous studies of this dissertation, pairs of chimpanzees and children had a limited amount of time to retrieve the rewards from the elevator before those were removed.

The main interest of this last study was to explore whether chimpanzees and children would overcome a Prisoner's Dilemma. The main interest was to investigate whether individuals would behave in a strategic manner, showing higher latencies to cooperate when that could lead to the loss of rewards. As in the previous studies, I was also interested in the strategies that these species would use to coordinate their decisions depending on the condition presented (i.e., whether individuals will engage in mutual cooperation or would rather take turns to reciprocate and divide their rewards). Finally, in the case of children, I explored the role of communication when children pairs needed to overcome a situation of competing interests.



# CHIMPANZEES COORDINATE IN A SNOWDRIFT TASK

## *2.1 Introduction*

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, 1994b, 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 in a variety of situations (Chalmeau, 1994; Cronin, Bridget, van Leeuwen, Mundry & Haun, 2013; Hirata & Fuwa, 2007; Melis et al., 2006a; Suchak, Eppley, Campbell & De Waal, 2014; Suchak, Eppley, Campbell, Fieldman, Quarles & De Waal, 2016). To a certain extent, chimpanzees can also coordinate their actions to obtain a high-value reward when there is an alternative (though lower-value) reward that can be obtained individually (Duguid et al., 2014). Even when a conflict of interest was introduced by presenting chimpanzee pairs with an unequal (5-1) and an equal (3-3) reward distributions, pairs still cooperated in the majority of trials (Melis et al., 2009). In contrast, Bullinger, Melis and Tomasello (2011b) found that chimpanzees preferred solitary over social work to obtain the same amount of food. This preference, however, was reversed when the payoff of the social option was higher than the non-social option.

In previous studies that did not offer subjects an alternative non-social option (but see Bullinger et al., 2011b), 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, initiating the action and investing energy in a cooperative act is not necessarily the best strategy from an individual's perspective. For instance, in the case of chimpanzee cooperative hunts, 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. 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 et al., 2012).

These types of interactions have been modelled by theorists in the Snowdrift game (Doebeli & Hauer, 2005; Kun et al., 2006; Sudgen, 1986). The Snowdrift is an anti-coordination game in which the best strategy is to do the contrary of your opponent. Therefore, in such dilemmas individuals have a common goal that can be either achieved by performing a cooperative act (either unilaterally or mutually) 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, the chimpanzee would prefer to begin the hunt rather than let the monkey escape. So, unlike in other scenarios such as 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.

The aim of this study was to use the Snowdrift game to investigate how chimpanzees solve a coordination task with a conflict of interest. For this purpose, pairs of chimpanzees were presented 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 unilaterally (only one chimpanzee pulls the rope) or collaborate (both chimpanzees pull and thus share the load). Alternatively, they could free-ride while the other did the work. Importantly, chimpanzees were free to decide the amount of weight they pulled. Therefore, collaboration, 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 pair. This adjustment was aimed to reflect real life situations such as cooperative hunts where 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 this has not been empirically demonstrated. Therefore subjects are not only faced with a binomial decision (either cooperate or free-ride) as in the majority of previous cooperative games (Chalmeau, 1994; Duguid et al., 2014; Hirata & Fuwa, 2007; Melis et al., 2006a,

2009) but can adjust their actions by investing different amounts of effort, allowing them to make precise decisions based on the physical contingencies and the partners' actions. Importantly, in this task there was no need for mutual cooperation as both subjects could get the same amount of food as long as one chimpanzee pulled. However, if neither pulled within a certain time-frame both lost the food. This set-up reflects the payoffs of the 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 this 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).

The main interests of the study was 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. Weight and time were manipulated to approximate the contingencies of chimpanzee hunting: the weight modelled the apes' costs to initiate the action while the time aimed to reflect the limited availability of the prey. Chimpanzees acting strategically were expected to wait longer to pull when the costs of pulling the tray were high –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 chimpanzees were expected to pay less attention to their partners' actions and thus wait less to pull. Finally, chimpanzees were also expected to wait longer in long time trials as they would have more opportunity to free-ride compared to short time trials. The study consisted of two test phases: all chimpanzees completed the test with one partner first before partners were re-shuffled for a second round. This manipulation served to study the overall effect of experience and whether chimpanzees 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.

## 2.2 Material and Methods

### *Subjects*

We tested seven females and five male captive chimpanzees ( $X_{\text{age}}=23.4$ ; see Table A1 in the Appendices for more information) housed at the Wolfgang Köhler Primate Research Center in Leipzig Zoo, Germany. In the first phase of the study all 12 made up six unique pairings. In the second phase, 10 of the 12 made up five new pairings. The experimental set-up required subjects to be in the same cage during testing. Consequently, only chimpanzees with a high degree of tolerance could be paired. Additionally, chimpanzees were paired according to similar weight (as a proxy for strength).

### *Material*

The task required subjects to obtain out-of-reach food rewards (one 4 cm banana piece for each individual) by pulling on ropes to move a tray (54.5X24 cm) (positioned on a fixed table (62.5 X 50 cm)) towards them (Figure 4; movement 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. This weight was created by the friction of a pair of brakes connected to a training-bike wheel (23 cm of diameter). 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. During trials, digital cameras recorded the weight measurements displayed on each of the scales. Then, the measurements were averaged for each individual per trial.

A 1 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 and/or 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.



The food rewards were placed in small bowls (10 X 10 cm) 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 (Figure 4; movement 2).



Figure 4. Experimental set-up. Both chimpanzees can either pull or not from their ropes to move the tray and retrieve the rewards (movement 1); at the same time the bowls move towards the edge of the tray (movement 2).

### *Procedure*

Chimpanzees were tested in a within subjects design in the high and low weight conditions (between sessions) and long and short trials (within sessions). At the start of a trial, one experimenter released the security peg. Next, experimenters baited the trays. During short time trials, one experimenter started to pull the invisible line after baiting the rewards.

### *Training*

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 social training session to understand and experience all three possible outcomes during the following test phase. During both training sessions (individual and social) 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 eight 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 eight times to receive the rewards (both sides of the apparatus were baited). Each subject pulled four times (two 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 social training and the test sessions).

#### *Social training*

Each pair 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 eight trials only one subject had access –four trials for each. During this training session, chimpanzees experienced more trials where they had to pull compared to trials where they did not pull. However, it was necessary for 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 the reward. The pulling side could not be controlled as in the individual training because the chimpanzees were free to move between sides although the amount of trials per

condition that each chimpanzee pulled was controlled, by waiting until both chimpanzees were positioned in front of the apparatus.

### *Test sessions*

Each pair performed eight test sessions: four heavy weight sessions (mean weight of tray = 70.64 kg) and four light weight sessions (mean weight of tray = 26.96 kg). Each session consisted of eight 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, their positions at the beginning of each trial were not counterbalanced. Prior to each test session subjects were given two individual trials to experience the weight they were going to face in the subsequent session. 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, subjects were expected 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. Based on the weight pulled by both subjects, we calculated a "measure of equality" (ME) to evaluate all possible instances of cooperation between individuals. To measure the ME we calculated the average of the weights (higher than 1.5 kg to avoid noise produced when subjects were just holding the rope) shown on the scales while the subjects were pulling from their ropes. Then, the difference between averages of the two subjects was divided by the sum of both averages. This resulted in a ME, ranging from -1 to 1. We transformed all of the values to positive values for analysis ( $1 - \frac{\sum W_1 - \sum W_2}{\sum W_1 + \sum W_2}$ ). Thus, an ME of 1 indicated perfect collaboration (subjects pulled an equal weight) while 0 indicated complete free-riding (only one individual pulled). Importantly, by using this measure, we identified 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 pair to pull. 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). This was possible as all sessions were recorded with digital cameras that allowed calculating times up to  $\frac{1}{25}$  of a second. Subjects change of behaviour between partners ( $N=10$ ) was tested based on the weight chimpanzees moved with different partners.

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 an index 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. This index ranged from 0 (no pull in all previous trials) to 1 (pull in all previous trials). Importantly, the first trial of each session was not taken into account as there was no previous experience.

The inter-observer agreement was excellent based on the 15% of the data ( $R^2 = 0.99$ ) and latencies ( $R^2 = 0.94$ ).

## 2.3 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:  $\chi^2_1 = 6.127$ ,  $N = 586$ ,  $p = 0.013$ ,  $CI [-0.195, -0.022]$ ; Figure 5a). 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:  $\chi^2_2 = 1.265$ ,  $N = 166$ ,  $p = 0.26$ ). Moreover, when the total time that chimpanzees spent pulling was analysed, they decreased their time during the last trials of high weight sessions (Model 3; LMM:  $\chi^2_1 = 10.76$ ,  $N = 586$ ,  $p = 0.001$ ,  $CI [0.047, 0.188]$ ; Figure 5b) further suggesting that waiting was strategic and not a consequence of fatigue.

However, despite indications of strategic behaviour, we found that collaboration (i.e., pulling together or a  $ME > 0$ ) was the dominant strategy to solve the task: 60% trials in low weight and 79% in high weight. Collaboration tended to increase across high weight sessions although the result was not

significant, (Model 4; GLMM:  $\chi^2_1 = 3.518$ ,  $N = 702$ ,  $p = 0.06$ ,  $CI [-1.911, -0.108]$ ; Figure 5c), which suggests that chimpanzee pairs tended to cooperate more often when the effort was high.

While collaboration 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:  $\chi^2_8 = 9.716$ ,  $N = 490$ ,  $p = 0.286$ ). However, the percentage of weight pulled by the first puller increased across sessions in the high weight condition (Model 6; LMM:  $\chi^2_1 = 7.252$ ,  $N = 478$ ,  $p = 0.007$ ,  $CI [-0.103, -0.021]$ ; Figure 5d) 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.

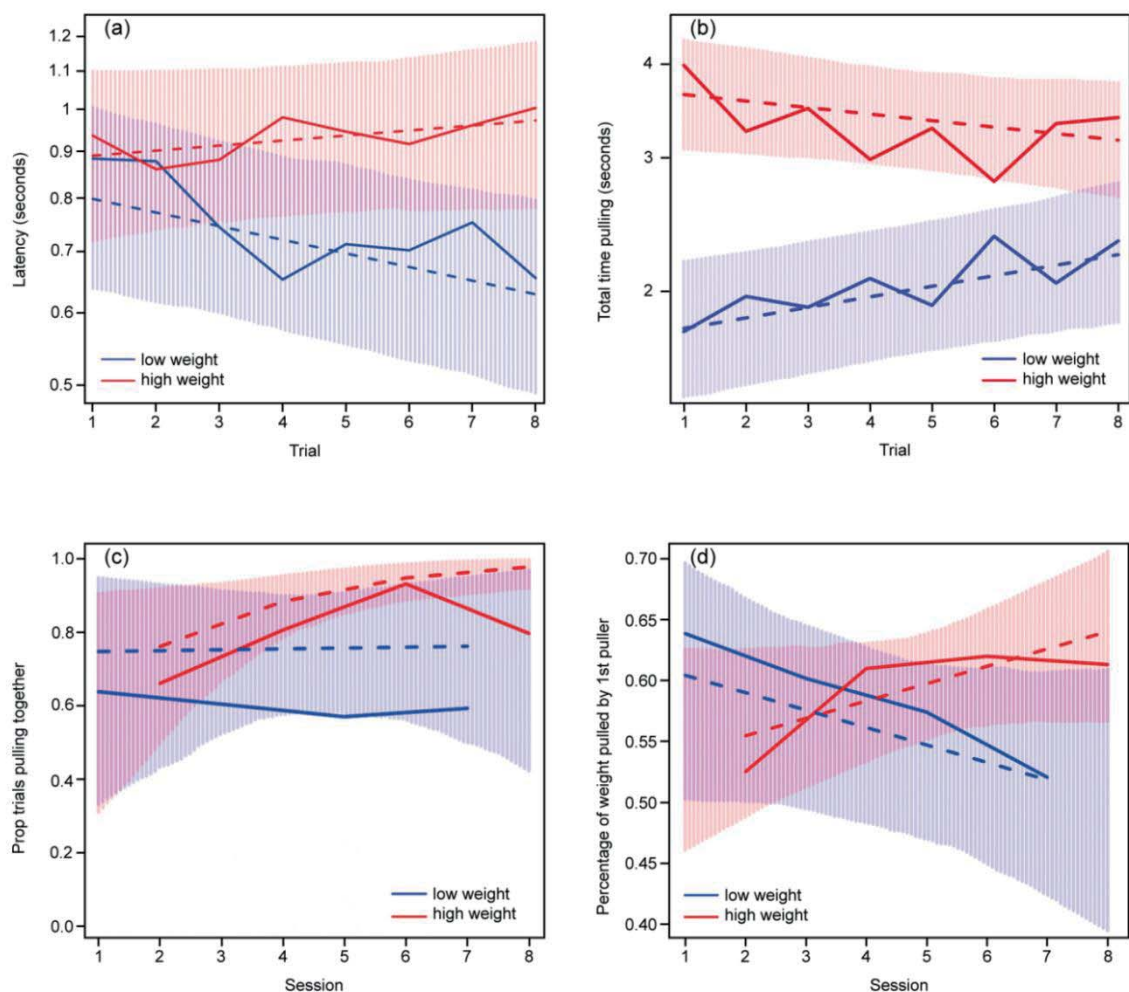


Figure 5. a) Latency to pull the tray in high and low weight conditions across trials; b) Time spent pulling the tray in high and low weight condition across trials after starting the action; c) Proportion of trials that subjects pulled together in high and low weight conditions across sessions and d) 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%.

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 the 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:  $X=45.89$ ,  $CI [27.84, 63.56]$ ; see the Appendices for more information about this model) suggesting that chimpanzees did not act in the same way when they were paired with different partners. Figure 6 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.

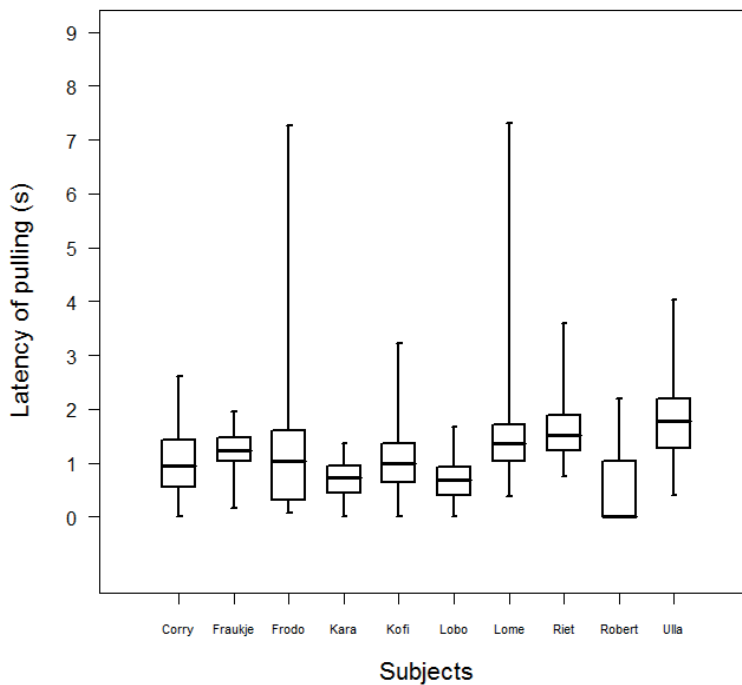


Figure 6. Pulling latencies (in seconds) for all subjects.

The *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. See the Appendices for further details of model construction and model results.

## 2.4 General Discussion

In a task where chimpanzees could potentially free-ride and benefit from their partner's actions, pairs solved the coordination problem by pulling together (i.e., mutual cooperation or collaboration), with a tendency to pull more often together when those costs were high. However, there were also indications that chimpanzees acted strategically to minimise 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 it was 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 (Bullinger et al., 2011a; Duguid et al., 2014). Here it has been 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 social 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 no differences in their latency to pull between conditions would be expected. On the contrary, subjects behaved strategically when pulling high weights. Moreover, it was not expected that cooperation tended to increase across sessions when subjects had already experienced in the social training that they could obtain food without pulling, but it increased over time in the high weight condition suggesting that subjects collaborated 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 less 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 mutual 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 mutual 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, Frigaszy & Visalberghi, 2005). Finally, it is also possible that the high rates of mutual cooperation that were found in the task were due to the high degree of tolerance between the members of the pair selected for the study (Hare et al., 2007). This suggestion needs to be corroborated by further studies testing pairs that differ significantly in their affiliative relationship.

Contrary to the study expectations, time played no crucial role. It is possible that the trial duration was too long (10 or 40 seconds) to influence subjects' decisions, which were made quickly (mean time to start pulling = 0.84 seconds), so there was never any real time pressure despite the salient movement of the dishes. 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 pairs 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). These results are in line with previous evidence which show that chimpanzees can differentiate between their partners' behaviour in cooperative tasks (Melis et al., 2006a; Engelmann & Herrmann, 2016).

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, chimpanzees were expected not to pull and thus completely free-ride. This result helps to explain why they acted strategically by waiting and pulling less weight as second pullers, while still cooperating frequently.

When the strategies used by chimpanzees in this study were compared to those human adults employ when they are presented with a Snowdrift game, 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 pair 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 this 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 from this study lived in the same group, experienced the loss of potential gains, and were able to decide how much effort they invested in pulling. To help explaining these possible differences between chimpanzees and humans, in the following chapter, I compare how apes and developmentally matched human controls (i.e., 5-year old children) 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, 2007; Melis et al., 2006a,

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. 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 this task mutual cooperation was not required to obtain the rewards but they still pulled together.

Moreover, Bullinger et al. (2011b) found that chimpanzees preferred to work alone rather than with a partner to obtain the same rewards in a cooperative task. In contrast, in this task 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 this 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 and colleagues (2011b) 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., 2011b), avoiding the risk of defection by the partner in the cooperative task. However, in the current task where cooperation is not necessary to obtain a reward, chimpanzees still cooperate in many trials. These contradictory results can be reconciled if they are considered in terms of risk avoidance and cost reduction. In Bullinger et al. (2011b) 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 a simplified version (the 2-person Snowdrift game) of the type of decision they would need to make to coordinate in the wild when conflicts of interest between group members are involved; *collective action problems* (CAPs) (Kitchen & Beehner, 2007; Nunn, 2000; see Schneider et al., 2012) such as border patrols (Watts & Mitani, 2001) or group hunting (Boesch, 1994b, 2002 although see Gilby et al., 2015 and Tomasello, 2009 for other interpretations). In these situations, some individuals can 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 of CAP each subject can potentially adjust their degree of investment and minimise costs while maintaining successful coordination as it has been observed in the present study.

In summary, in a task where free-riding was possible, subjects chose to mutually 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.



# CHIMPANZEES, BONOBOES AND CHILDREN SUCCESSFULLY COORDINATE IN CONFLICT SITUATIONS

## *3.1 Introduction*

Many animal species regularly face situations in which individuals need to coordinate to overcome conflicts of interest. Most research has focused on how groups decide on the direction of travel when individuals have differing preferences (Couzin, Krause, Franks & Levin, 2005; King & Sueur, 2011; Strandburg-Peshkin et al., 2015) but, as with humans, there are many other contexts involving a conflict of interest. For instance, lions (Heinsohn & Packer, 1995) during inter-group encounters or chimpanzees (Boesch, 2002) that lag behind in cooperative hunting events waiting for others to start the chase may avoid fighting, injuries and energy expenditure (Gilby & Connor, 2010). But if everyone waits, no hunt will ensue. Recent evidence suggests that some chimpanzees solve the coordination problem by starting the hunt and thus paying the initiation costs (acting as “impact-hunters”) (Gilby et al., 2015). However, it remains unclear whether the benefits that “impact-hunters” obtain from the hunt outweigh the initiation costs. In other words, it is unclear whether these subjects strategically take into account the potential costs and benefits of the hunt when they initiate it.

Situations of the type described above can be understood as CAPs (Kitchen & Beehner, 2007; Nunn, 2000), or at the dyadic level, as Snowdrift games (Doebeli & Hauer, 2005; Kun et al., 2006; Rapoport & Chammah, 1966; Sudgen, 1986). The Snowdrift occurs when an individual (A) would prefer another individual (B) to carry out a costly action that benefits both A and B. However, if B does not act, it is better for A to act alone rather than not act at all. Therefore the preference for A would be 1<sup>st</sup>) to wait for B to act, 2<sup>nd</sup>) divide the cost by acting together and 3<sup>rd</sup>) pay all the cost of the action. One crucial difference between the Snowdrift and other classical games such as the Prisoner’s Dilemma (Axelrod, 2006) is that the worst case scenario in the Snowdrift game occurs when both partners defect while in the Prisoner’s Dilemma occurs when the individual cooperates but the partner defects. Consistent with the idea that cooperation is less risky in a Snowdrift than in Prisoner’s Dilemma, both agent-based simulations (Kümmerli et al., 2007) and human behavioural experiments (Duffy & Feltovich, 2002, 2006) have found higher and more stable levels of cooperation in Snowdrift than Prisoner’s Dilemma.

In general, models in which mutual defection is the worst-case scenario offer a better explanatory model of the emergence of cooperation and helping in natural conditions (Bshary et al., 2016). Although models like the Stag Hunt (Skyrms, 2004) show crucial differences between the way chimpanzees and humans manage the challenge of coordinating actions and maintaining high levels of cooperation (Duguid et al., 2014; Tomasello et al., 2012), Snowdrift models seem a better fit for situations in which chimpanzees need to coordinate actions towards common goals (Chalmeau, 1994; Hirata & Fuwa, 2007; Melis et al., 2006a; Suchak et al., 2016), especially as soon as there is conflict of interest. Recently, Grueneisen and Tomasello (2016) have investigated how five-year old children coordinate their actions in a Snowdrift game. The study presented pairs of five-year old children with a different version of a Snowdrift: two toy trains with rewards in the cargo. Each child controlled one train which had to arrive at its own station positioned behind the partners train to retrieve the rewards. However, if both trains continued along the track they were on, they would crash into each other before arriving to their stations and all rewards would be lost. Thus, one child needed to swerve onto a side track at the cost of some cargo. Therefore, it was in each child's interest to wait for the partner to swerve. Children rarely crashed the trains by taking turns swerving.

Grueneisen and Tomasello (2016) study is in line with the previous study presented in this dissertation (Study 1 in Chapter 1). Yet, although these two studies demonstrated that both species can solve Snowdrift dilemmas, they are not directly comparable because chimpanzee pairs had the option to collaborate and share costs within trials (Study 1), whereas children did not (Grueneisen & Tomasello, 2016). Consequently, the current study presented children and two ape species, chimpanzees and bonobos, with the same Snowdrift game paying special attention to any indication of strategic decision-making (i.e., waiting to pull). Although bonobos have not been studied in Snowdrift dilemmas, previous studies on cooperation indicate that they performed better than chimpanzees under some conditions that required higher tolerance towards conspecifics (Hare et al., 2007). Study 2 investigated subjects' decisions in a Snowdrift and a *competitive* condition. The best strategy in the Snowdrift condition was to wait for a partner to pull and thus obtain the higher of two rewards. However, as in the classical Snowdrift situation, it was better to pull if no-one pulled. The Snowdrift was compared to the *competitive* condition, which required subjects to pull faster than the partner to obtain the higher reward. If subjects behaved strategically, a higher latency to pull was expected in Snowdrift than in *competitive* and a higher frequency of both individuals pulling in *competitive* than Snowdrift. Finally, based on a recent study (Duguid et al., 2014), communication was expected to play a role in children's coordination but not in chimpanzees or bonobos. Afterwards, a follow-up study was conducted with apes (Study 3) because some individuals consistently refused to pull in both conditions. Thus, to investigate whether this behaviour was strategic or some individuals were just

content with the food received, we presented chimpanzees and bonobos the same apparatus (and conditions) as in Study 2 with the addition of an alternative option for each individual. We hypothesized that this would allow subjects to better manage the risk by choosing the alternative option depending on the options available in the apparatus and their partner's preferences.

### *3.2 Material and Methods: Study 2a*

#### *Subjects*

We tested ten captive chimpanzees (5 females;  $M_{age}= 20.5$  years) and 6 captive bonobos (5 females;  $M_{age}=13.7$  years) housed at the Wolfgang Köhler Primate Research Center in Leipzig zoo (see Table A6 in the Appendices for more information about the subjects). During the first phase of the study, the chimpanzees made up 5 unique pairs and the bonobos made up 3 unique pairs. In the second phase pairs were reshuffled to create 5 new chimpanzee pairs and 3 new bonobo pairs.

#### *Materials*

Pairs of apes were presented with a rotating tray (91x10 cm) (Figure 7) attached to a platform (88.5x96.5 cm) placed between two rooms. Each end of the rotating tray was baited by different amounts of fruit (banana slices for chimpanzees and half grapes for bonobos). Subjects faced each other across the platform, each with access to one side of the apparatus. Two identical ropes (76 cm) were attached to the interior end of the tray with Velcro and fed into each subjects' room. Subjects could access the apparatus via a small window on either side of the platform; the experimenter opened these windows at the start of a trial but the windows remained closed between trials. Apes could only access the interior or the exterior end of the tray by pulling the rope towards them or by waiting for the partner to pull from the other side, respectively. Thus, when a subject pulled its rope, the roped end of the tray rotated towards her while the free end rotated towards her partner.

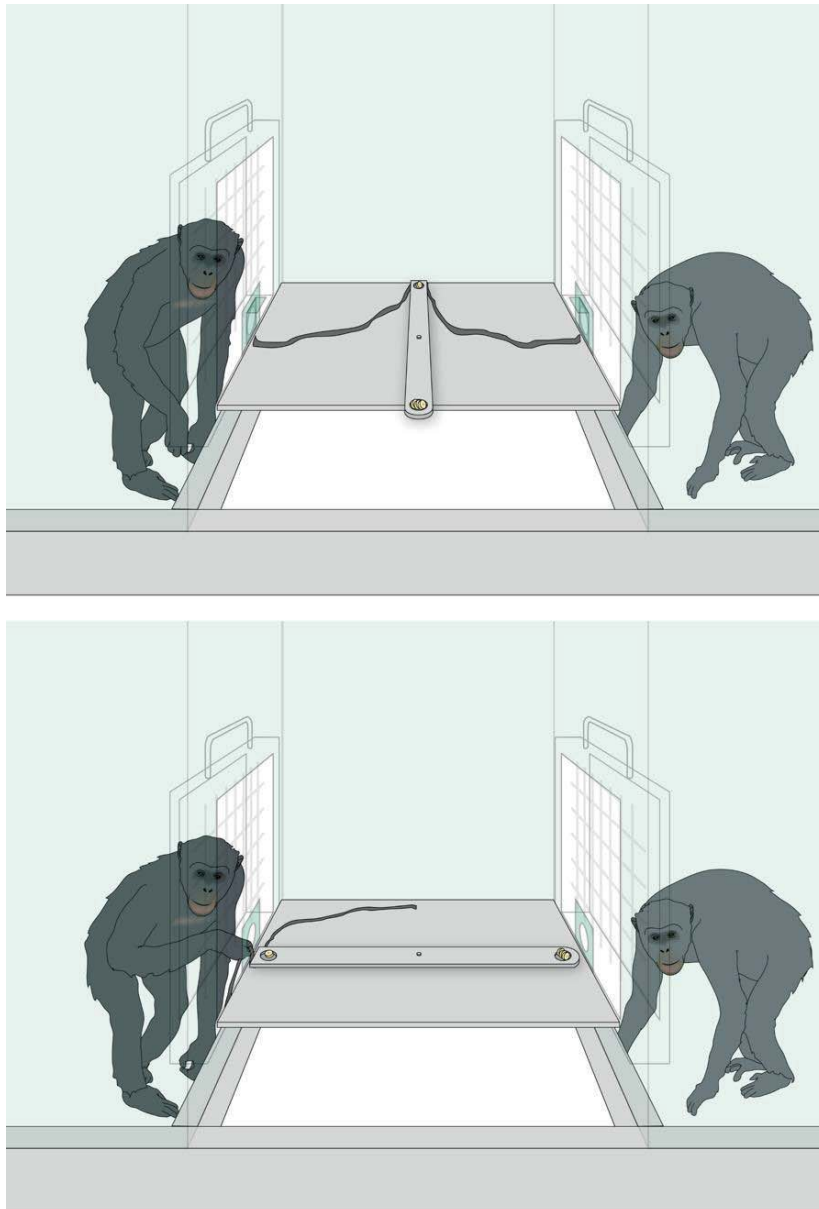


Figure 7. Experimental set-up of Study 2a.

### Procedure

We used a within-subjects design with two conditions (Snowdrift & *competitive*). In the Snowdrift condition, we placed one piece of fruit on the roped end of the tray and four pieces on the free end, thus creating a Snowdrift dilemma because the subject's best choice was to wait for the partner to pull and bring the free end within her reach. In the *competitive* condition, we placed the four pieces of fruit on the roped end while the free end was baited with one piece. In this condition subjects should pull faster than their partner to obtain the higher reward.



At the start of a trial, two experimenters allowed subjects access to their respective ropes by opening the windows. The subjects then had 30 seconds to pull the rope and get the rewards placed on the rotating tray or wait for the partner to pull. If no ape pulled after the 30 seconds, the experimenter removed all rewards and ended the trial. In case both individuals pulled simultaneously, one or both ropes disconnected from the tray resulting in a random movement and a possible loss of all rewards.

### *Individual training*

This training phase served to show the subjects the main contingencies of the apparatus and how to access the rewards. Subjects were required to pull the tray to retrieve food (only one of the two ropes was attached to the tray at a time). After pulling the rope subjects could access both rooms and retrieve the food from both sides of the apparatus. Within each session subjects completed two trials in each condition from each side of the apparatus for a total of four Snowdrift trials and four *competitive* trials, in a predetermined random order. Each subject performed two sessions on separate days.

### *Social training*

This training served to demonstrate that, depending on the condition, subjects could get either high or low rewards by either pulling themselves or by waiting for a partner to pull. Subjects were trained in the pairs that they would be in during the first phase of the test sessions. They experienced all four possible outcomes: obtain the high or the low reward by pulling (Snowdrift and *competitive* conditions respectively); or obtain the high or the low reward by waiting (*competitive* and Snowdrift conditions respectively). Subjects were in adjacent rooms and the door between them was closed. A trial started after an experimenter checked that subjects were looking when the food was placed on the tray. If subjects were not looking they were called by the experimenter. After placing the rewards, the experimenters opened the windows. Each pair had two sessions (on separate days) of eight trials each. Subjects experienced all possible combinations from both sides of the apparatus (swapping their position between sessions). As in the individual training, only one rope was attached to the tray during a trial.

### *Test sessions*

After completing the training phases, each pair received eight 8-trial test sessions (four trials per condition in a randomised order). Subjects only received one session per day and switched sides between sessions. Test sessions were identical to the dyadic training sessions except that both subjects had access to their own rope. After completing eight sessions with their first partner (phase 1) each subject was paired with another one for another eight sessions (phase 2).

### *Coding*

Our measure of coordination success was the percentage of trials in which pairs succeeded, defined as trials in which at least one member obtained a reward. We scored three further dependent variables: subjects' latencies to pull, their pulling rate (derived in three different measures) and communication. We defined the latency to pull as the elapsed time between the opening of the doors and the first pulling action. We defined a pulling action as either the first instance of tray movement towards a subject or the first instance of tension between the ropes of both subjects, which occurred when both subjects pulled simultaneously. Communication was defined as any vocal or gestural communicative acts directed towards the partner or the partner's actions during test trials. Vocal communication was defined as any vocalization directed towards the partner or the partners' actions. We included screams and whimpers. Screams were defined as loud, high-pitched sounds that apes directed towards the partner or the partners' actions. Whimpers were defined as low, feeble sounds expressing fear (moans) directed towards the partner or the partners' actions. We also coded claps (attentional getter) as gestural communication. Claps were defined as sounds resulting of the repeated strike of individuals' hand palms.

We calculated three measures derived from the subject's pulling rate. First, we considered whether apes behaved strategically by comparing the number of strategic choices (i.e., the proportion of pulls in the *competitive* condition plus the proportion of non-pull decisions in the Snowdrift condition) to the levels expected by chance. With this information, we also classified subjects as *pullers* (pulling  $\geq$  75% of trials in both conditions), *non-pullers* (pulls  $\leq$  25% of trials in both conditions) and *strategisers* (*competitive* pulling > Snowdrift pulling resulting in a food intake significantly above chance in both conditions). Second, we scored conflict trials defined as both subjects pulling simultaneously and investigated whether their likelihood of occurrence increased by the occurrence of a conflict in the previous trial. Finally, we investigated subjects' flexibility defined as the change in pulling behaviour

shown between subjects. To do that, we required a comparison of the subject's frequencies of pulls per condition with each partner.

The inter-observer reliability was excellent based on the 20% of the data (time of pulling:  $r = 0.99$  for both species; 1.1 % of data mismatch between observers in bonobos and 2.5 % in chimpanzees).

### 3.3 Results

Overall, pairs of apes obtained the rewards in 98% of trials. Subjects waited longer to pull during Snowdrift than in *competitive* trials (Model 9; LMM:  $\chi^2_1 = 9.181$ ,  $N = 1019$ ,  $p = 0.002$ ,  $CI [0.057, 0.483]$ ; Figure 8). From their pulling rates, four subjects were classified as *pullers*, three as *non-pullers* and two as *strategisers*. The remaining seven subjects were unclassified. The two *strategisers* (one male chimpanzee and one female bonobo) pulled in *competitive* trials and not in Snowdrift trials (binomial test,  $p < 0.005$ ), a behaviour that resulted in a maximization of their payoffs (Table A12 in the Appendices). However, when the strategies at the dyadic level were considered a different picture emerged. In nine of 16 pairs one subject pulled in most of trials (>75%) while the other almost never pulled (<25%). Thus, a high proportion of pairs displayed a strategy based on only one subject pulling in both conditions. Pulling rates also indicated that apes were more likely to pull simultaneously in *competitive* than Snowdrift trials (Model 10; GLMM:  $\chi^2_1 = 6.607$ ,  $N = 895$ ,  $p = 0.01$ ). Previous conflict trials had no effect on their subsequent response (Model 10; GLMM:  $\chi^2_1 = 1.636$ ,  $N = 895$ ,  $p = 0.2$ ). Subjects' behaviour changed between partners: 31% of subjects modified their behaviour (i.e., subjects varied in more than 50% their pulling rates between partners; Figure 1A in the Appendices). Finally, it was found that apes almost never communicated with their partner to solve the task (individuals protested, uttering screams and whimpers, on 0.01 % trials). See the Appendices for further details of model construction and model results.

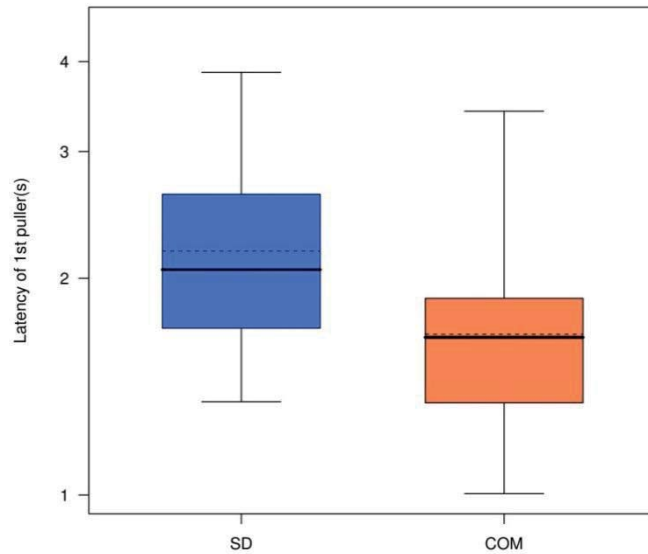


Figure 8. Latency of the 1<sup>st</sup> puller to pull the rope in Snowdrift (SD) and competitive (COM) trials. The dotted lines represent the fitted model. Latencies in seconds are presented in a logarithmic scale.

### Discussion

Chimpanzees and bonobos came up with an efficient, simple solution to coordinate in this task, the “only-one-partner-pulls” strategy. Although this strategy prevented subjects from maximizing their own payoffs, the randomised presentation of the rewards led to an almost equal division of rewards between partners. Moreover, two subjects behaved strategically although it was unclear why so few did so (2 out of 16 individuals) and what strategic level their decisions entailed. Next, 5-year old children were presented with the same basic task to compare their strategies to those of apes (Study 2a) and subsequently probed apes strategic behaviour further by varying potential payoffs for the subject and the partner in Study 3.

### 3.4 Material and Methods: Study 2b

#### Subjects

We tested twenty pairs of 5- to 5.5-year old children (10 pairs of girls and 10 pairs of boys) in kindergartens in the Leipzig area.

### *Materials*

In general, pairs of children were presented with the same task as chimpanzees and bonobos (Figure 9). The apparatus was a wooden box with a lid that prevented children from directly accessing the rewards (60X60X25 cm). The box was placed on the ground between both children. Access to the ropes was blocked by two sliding doors. Only Experimenter 1 could open them to allow access at the start of the trial. In contrast to Study 2a, the rewards were not collected from the rotating tray (54X10 cm) but fell through a hole to the ground, in front of each child. In the children's version of the apparatus we added a small peg under the rotating tray to prevent it spinning 360°. In contrast to apes, children collected tokens (wooden blocks during training and more valuable plastic marbles ("jewels" of four different colours) during test sessions); this allowed children to monitor their own and their partners' rewards across the study.

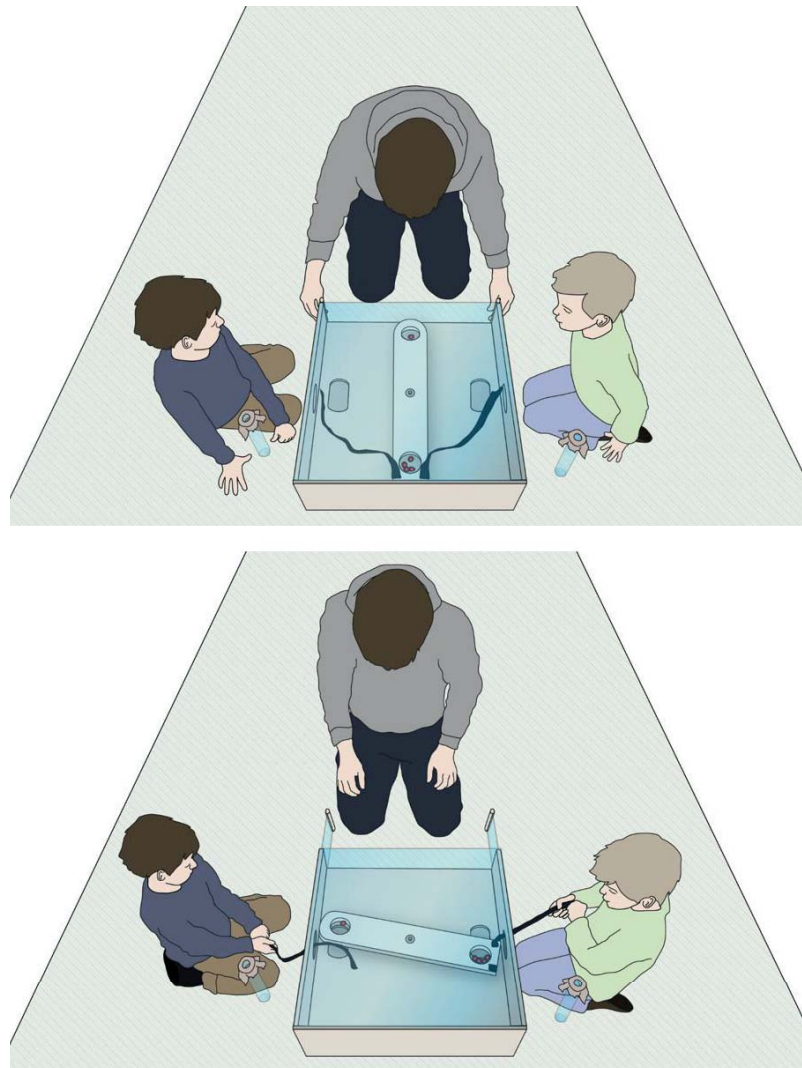


Figure 9. Experimental set-up of Study 2b.

### *Procedure*

At the beginning of a trial, children had time to check the reward distribution on the tray. Afterwards, the experimenter removed the two sliding doors simultaneously. After 30 seconds, the experimenter removed all the rewards and ended the trial.

### *Training*

Children were only trained and tested with one partner. In Study 2b we did not conduct individual training in order to reduce the testing time per dyad. However, during the first half of the social training session Experimenter 2 emphasized the rewards distribution with the aim of highlighting all possible outcomes that children could encounter during the test.

### *Social training*

The social training was essentially the same as in Study 1a except that children only performed one session of eight trials. Therefore, children swapped sides halfway through the session (between trials four and five). During the training children collected rewards (wooden blocks) they could insert into a box to produce music.

Prior to the social session, Experimenter 2 explained to the children that they would play a game that consisted of collecting “jewels” (the marbles) from a magic box. However, in order to collect the “jewels”, they were first required to remove the “stones” (the wooden blocks).

After the short explanation, Experimenter 2 entered the test room with the children and showed them the wooden box and introduced them to Experimenter 1. Each child took their position in front of the openings on the sides of the box. Experimenter 2 sat between the children, on the other side of the apparatus from Experimenter 1. Experimenter 2 told the children to insert the wooden blocks in the music box. At the end of each trial, Experimenter 2 pointed the opening of the music box towards each child to facilitate them to insert the blocks. During the training and the test sessions, Experimenter 1 relocated the ropes and baited the rewards between every trial. Experimenter 1 only instructed the children to swap sides between trials four and five of the training and the test sessions.

### *Test sessions*

After the training, each pair performed three test sessions on two consecutive days – apes received 16 sessions. The first session was conducted after the training and the second and third sessions were conducted on a second day. Each session consisted of eight trials and children swapped sides after completing trial four. Children received two *competitive* and two Snowdrift trials in a randomised order from each side of the apparatus. At the beginning of each trial, Experimenter 1 showed the reward locations to the children before allowing them to access to the ropes. In the test sessions, children collected their rewards and kept them in their own plastic tubes previously provided by the experimenters.

Prior to the first test session, Experimenter 2 presented the children with Plexiglas tubes. He told them that now they were going to collect “jewels” and instructed them to collect as many as possible and to put them inside their own tube. After the instructions, Experimenter 2 presented the apparatus again (which was already baited with the first set of marbles) and left the test room. At the end of the first session they were told to write their names on the tubes and to leave the tubes in the room for the next day. In the second test day and prior to the second session, Experimenter 2 briefly instructed the children again to collect “jewels” and give them their Plexiglas tubes. Between sessions 2 and 3, the children left the test room and waited for approximately 7 minutes with Experimenter 2 while Experimenter 1 reset the apparatus before children entered the test room again. At the end of the third session, every child chose four marbles to take home.

### *Coding*

We analysed the same dependent measures as in Study 2a, excluding flexibility because children only played with one partner. Additionally, we adjusted our coding to include verbal communication. We only analysed verbal communication related to the task by focussing on the five following types. *Imperative*: deontic verbs used to direct their partners’ actions (e.g., “You should pull”), *protests*: statements of disapproval and objection about a partner’s actions or intentions (e.g., “No, I also wanted”), *informative*: acts aimed at informing partners about a child’s current or impending actions or intentions (e.g., “I am going to pull now”), *turn-taking*: stating previous or future actions aimed at influence others’ decisions. This type of communication could be coupled with either *imperative*, *protests* or *informative* (e.g., “I pull because you pulled before”; “Next time you pull”) and *deception*: acts aimed at explicitly cheating their partners.

For every trial, we coded whether pairs communicated (by either one or both children). In every trial, a measure of 1 or 0 was given depending whether communication occurred or not. In addition, we coded whether each of the five categories of communication (*imperative*, *protests*, *informative*, *turn-taking* and *deception*) was present within a pair (uttered by either one or both children).

The inter-observer agreement for the timing of decisions based on the 20% of the data was excellent (pulling actions from child on the left side:  $r = 0.93$ , 1.5 % of data mismatches between observers; pulling actions from child on the right side:  $r = 0.99$ , 4% of data mismatches between observers). The inter-observer reliability for communication based on the 20% of the data was also excellent (Cohen's Kappa = 0.94).

### 3.5 Results

Overall, pairs of children obtained the rewards in almost all trials (99%). Children increased their latency to pull across sessions in Snowdrift trials and decreased it in *competitive* trials (Model 11; LMM:  $\chi^2_1 = 4.913$ ,  $N = 478$ ,  $p = 0.027$ ,  $CI [-0.023, 0.223]$ ; Figure 10) indicating that like apes, they distinguished the conditions. Based on their pulling rates, most children were classified as *pullers* (24 of 40) and one child was classified as a *non-puller*. Three children made strategic decisions significantly above chance (binomial test,  $p < 0.005$ ) by pulling in *competitive* trials and not pulling in Snowdrift trials. At the dyadic level, only one pair followed the “only-one-partner-pulls” strategy described for apes. Instead, most child pairs followed a “both-partners-pull” strategy regardless of the condition. In contrast to apes, children both pulled equally often in *competitive* (53 % of times together) compared to Snowdrift trials (43 % of times together) (Model 12; GLMM:  $\chi^2_4 = 5.305$ ,  $N = 420$ ,  $p = 0.257$ ). Finally, it was found that children communicated more often in Snowdrift than in *competitive* trials (Model 13; GLMM:  $\chi^2_1 = 4.719$ ,  $N = 480$ ,  $p = 0.03$ ,  $CI [-0.219, 2.464]$ ). Communication occurred in 32% of the trials (in 96 Snowdrift and 56 *competitive* trials out of 240 trials per condition; Figure 11). Although the distribution of children communicative types could not be statistically analysed, imperative utterances (e.g., “you should pull”) were mostly used in situations in which they needed a partner to act against the partners' self-interest (58% of 96 communicative acts in Snowdrift trials). In contrast, no communicative type predominated in competitive situations. See the Appendices for further details of model construction and model results.



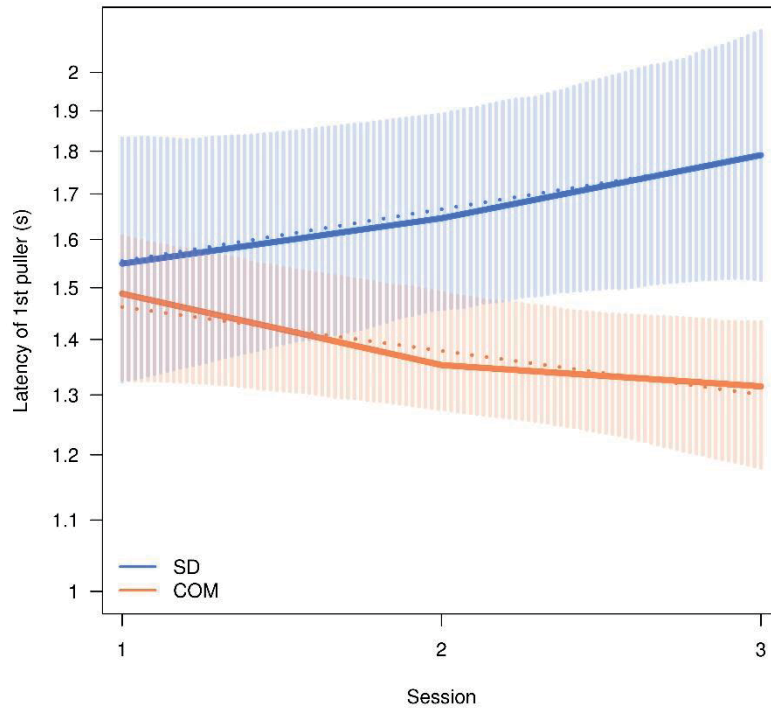


Figure 10. Latency of the 1<sup>st</sup> puller to pull the rope in SD and COM trials across the three test sessions. The dotted line represents the fitted model and the shadowed areas represent the CI at 95%. Latencies in seconds are presented in a logarithmic scale.

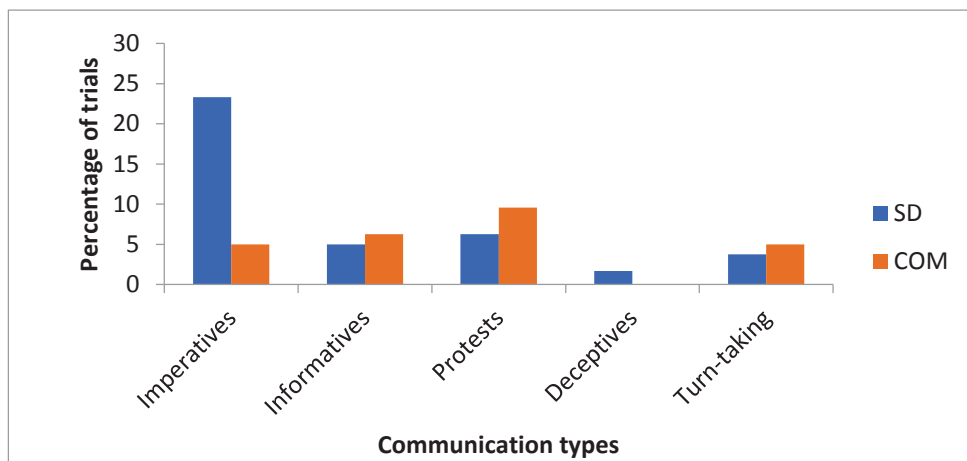


Figure 11. Percentage of trials in which every type of vocal communication occurred at least once within a trial.

In a comparison between children' and apes' strategies, the most strategic individuals were children. This is evident from Figure 12, which shows the proportion of strategic choices in *competitive* and Snowdrift trials. The upper right quadrant (above 50% strategic choices in both conditions) is clearly dominated by children. However, it is important to note that due to the reduced statistical power of

the children’s data (children performed three sessions while apes did sixteen) not all individuals in this quadrant performed significantly above chance, even though they made strategic choices more often than the apes categorized as *strategisers*.

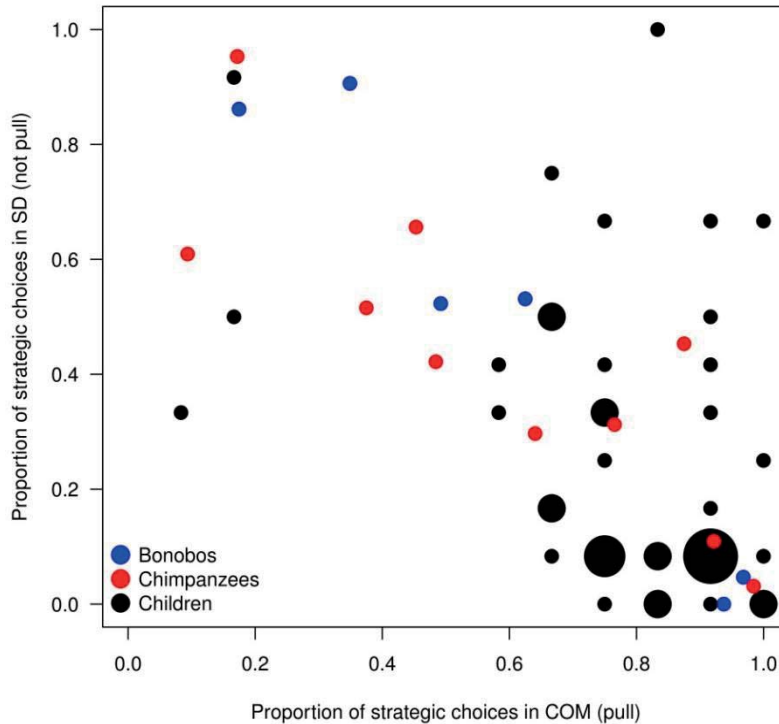


Figure 12. Proportion of strategic choices in both SD and COM trials for all subjects of the three species. The most strategic individuals in both conditions are in the top-right corner of the plot. The size of the dots represents frequencies of subjects for different scores.

### Discussion

Children were as successful as apes and made a similar proportion of strategic choices compared to apes (53% of strategic choices in children, 51% in chimpanzees and 54% in bonobos). However, they did so with much less experience with the task (24 compared to 128 trials). Unlike apes, we found that most children followed a “both-partners-pull” strategy regardless of the condition, which may not be that different in terms of complexity to the apes’ “only-one-partner-pulls” strategy. However, children showed more signs of strategic decision-making than apes: they used communication to influence their partner decisions and learned to distinguish both conditions after only three sessions (Figure 10).

### *3.6 Material and Methods: Study 3*

#### *Subjects*

We tested eight captive chimpanzees (3 females;  $M_{age} = 13.5$  years) and 4 captive bonobos (3 females;  $M_{age} = 13.5$  years) housed at the Wolfgang Köhler Primate Research Center in Leipzig zoo (see Table A12 in the Appendices for more information about the subjects). Seven chimpanzees and all bonobos had taken part in Study 2a. Each individual was tested with three partners. During the first phase of the study, the chimpanzees made up four unique pairs and the bonobos made up two unique pairs. In the second and third phase, pairs were shuffled to create another four new chimpanzee pairs and two new bonobo pairs per phase.

#### *Materials*

We presented pairs of individuals with the same apparatus used in Study 2a with two main additions. In this new set-up subjects needed to move a sliding door either to the left or the right side to access the apparatus. If they moved the sliding door to the right side they could access the ropes as in the original apparatus. However, if they slid the door towards the left they could directly access an alternative option (Figure 13). The alternative option consisted of a fixed platform (10X10 cm) attached to the Plexiglas frame located approximately 5 cm above the apparatus to not interfere with the rotation of the tray. A pin was inserted in the door to prevent subjects from sliding it open before the start of the trial. The experimenter could remove the pin before the trial started. When the door was opened to one side, another locking mechanism prevented it from being moved back to its original position. As a result, subjects could only make one choice per trial.

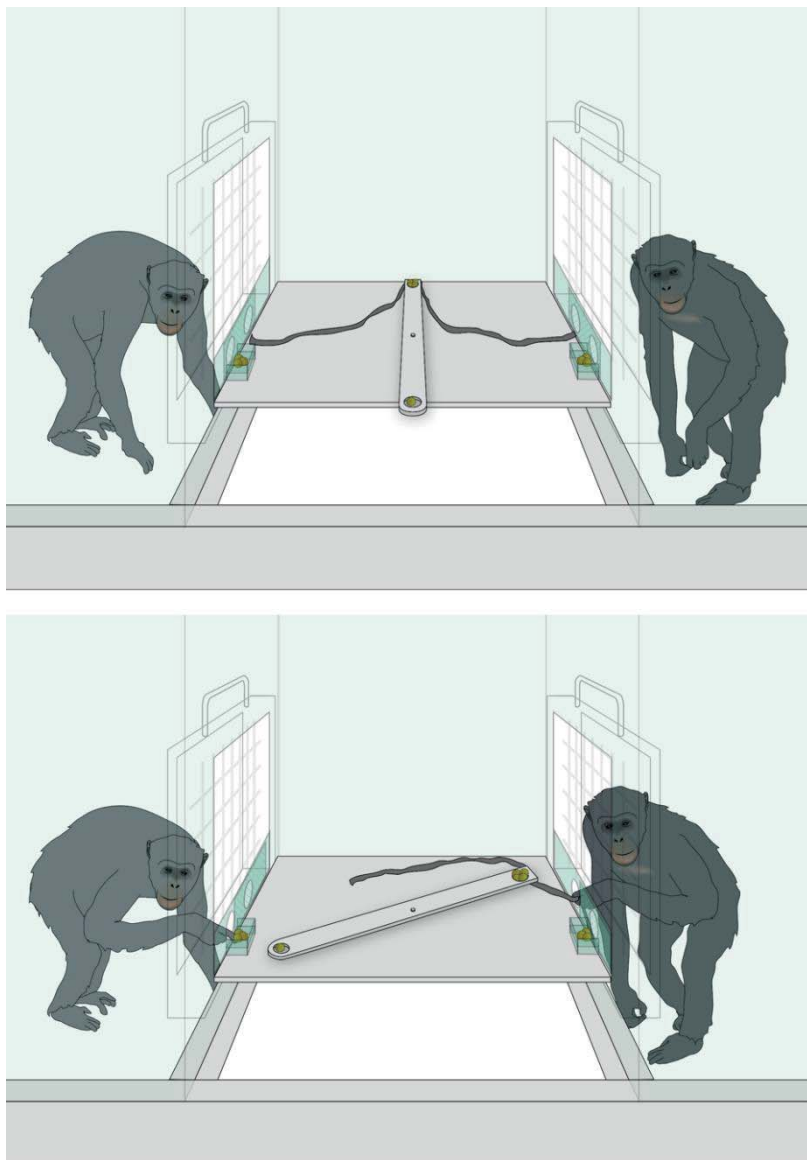


Figure 13. Experimental set-up of Study 3.

### Procedure

Subjects were tested in a within-subjects design in the same two conditions as Study 2a (Snowdrift and *competitive*). In this set-up the rotating tray was baited with one and five food pieces. The alternative platforms could be baited with either zero, one, three or five food pieces depending on the condition presented (non-social condition levels). Both alternative platforms were baited with the same food quantity on a given trial. Chimpanzees and bonobos received the same kind of food as in Study 2a.

At the beginning of a trial, two experimenters simultaneously removed the pin that had prevented choosing between options and apes had 10 seconds to make their choices. When a subject opened

the window to the alternative platform, they could immediately access the reward. When a subject opened the door to the tray they could either wait for the partner to pull the rope or pull themselves (as in Study 2a). An apes' choice for the rotating tray was defined as the "social option" and the alternative platform as the "non-social option".

### *Individual training*

This training phase served to show the subjects how to access the rewards.

Subjects were required to access the baited option and retrieve the reward. Within a session a subject faced eight trials presented in a randomised order: four trials in which only the rope end was baited and four trials in which only the alternative platform was baited with one piece of food (Figure 14, phase 1). The presentation side was counterbalanced between sessions.

Subjects had to choose correctly in at least 80% of the trials during two consecutive sessions to continue with the next phase. The same criterion was used for the rest of training phases.

### *Individual training 2*

This training served to demonstrate that subjects could either get a high or a low reward that could be placed on either the tray or the alternative platform.

Subjects were required to choose the option with more food and then retrieve the reward. Within a session a subject faced eight trials in a randomised order: four trials in which the rope end of the tray was baited with five pieces of food and the alternative platform with one, and four trials in which the alternative platform contained five pieces while the ropes' end was baited with one (Figure 14, phase 2). Subjects experienced all possible combinations from both sides of the apparatus, swapping their positions between sessions.

### *Individual training 3*

The purpose of this training phase was to ensure that the apes took into account all the quantities involved in a given trial. In this training phase the door that separated both sides of the apparatus was open to allow subjects access to both sides of the apparatus.

Within a session subjects were presented with two conditions, the social and the alternative condition (Figure 14, phase 3). Each subject was presented four trials of each condition in a randomised order. In the alternative condition both ends of the tray were baited with one reward each and the alternative platform with four. In the social condition each end of the tray as well as the platform were baited with two rewards. Thus, in the alternative condition a subject had to choose the alternative platform while in the social condition a subject had to forego the food present on the alternative platform (which was closer) and access the ropes, obtain the two rewards from the ropes' end and move to the other side of the room to retrieve the other two rewards from the free end. Subjects experienced all possible combinations from both sides of the apparatus. They swapped their positions between sessions despite the doors were open.

The baiting order differed between conditions. In the alternative condition the rewards were baited first on the alternative platform and then on the tray, always starting from the rope's end. The tray was always baited after the alternative platform to draw subjects' attention to it and to be sure that they paid attention to all the rewards.

In the social condition the platform was baited first on half of the trials and first the tray on the other half. This was done to control for possible attentional biases towards the last baited place.

### *Social training*

This training was the same as the dyadic training of Study 2a (phase 2).

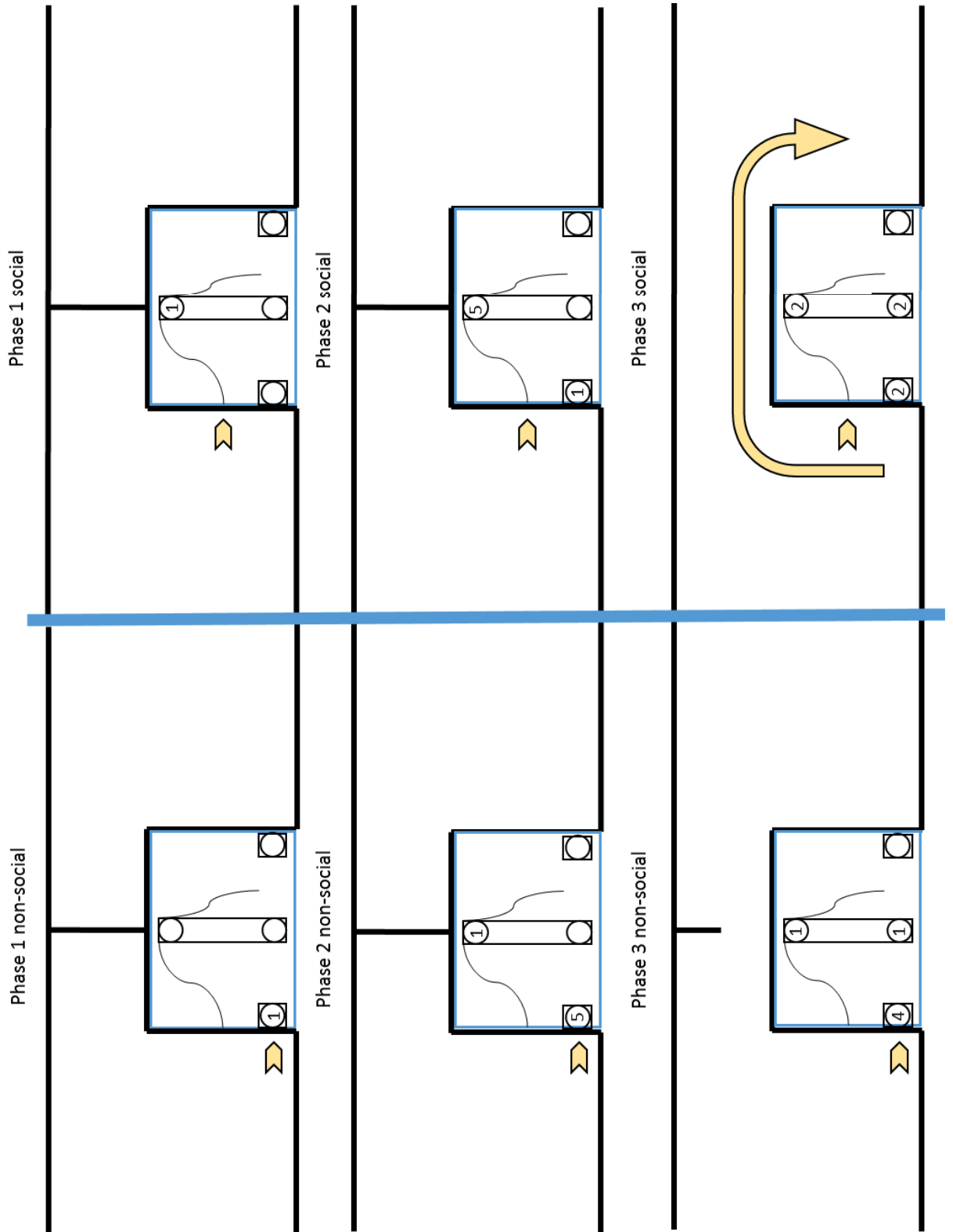


Figure 14. Training phases.

### *Test sessions*

After completing the training phases every pair performed eight test sessions. Each session contained four trials of each social condition presented in a randomised order. In the alternative platform, the levels of the non-social condition were randomly presented between sessions (staying constant within sessions), each level presented in two sessions. In the test sessions, both subjects had access to their own rope. Subjects switched sides between sessions. After the eight sessions with their first partner (phase 1) each subject was paired with two further partners for another two blocks of eight sessions (phase 2 and 3).

### *Coding*

We measured the percentage of successful trials (defined as in Study 2). Additionally, to study how chimpanzees and bonobos solved this new version of the game, we considered two main dependent variables: choices and latencies (further divided in two latency measures). Choices were defined as the proportion of trials in which each subject chose the social or the non-social option. The first latency measure consisted of the elapsed time between the pins' removal and the sliding of the door halfway to one side (at which point they could not change direction). The second latency measure was the elapsed time between accessing the social option and pulling the rope (defined as in Study 2a). These latencies allowed us to assess whether the 2<sup>nd</sup> actors made strategic decisions contingent on the previous action of the 1<sup>st</sup> actors during the same trial.

To determine 1<sup>st</sup> and 2<sup>nd</sup> actors, we only considered those trials in which both individuals acted at different times (those trials in which both individuals opened the door). The average time between 1<sup>st</sup> and 2<sup>nd</sup> actors was less than 2 seconds. Then, for each combination of social and non-social conditions (8 combinations, see Table 1) the strategic choices of the 2<sup>nd</sup> actors based on the combination of social and non-social options was categorized. Moreover, we took into account those instances where the 2<sup>nd</sup> actors could maximize their rewards by taking into account the previous action of 1<sup>st</sup> pullers (see the two combinations of non-social option 3 in Table 1). In other words, in these two combinations 2<sup>nd</sup> actors strategic choices differed depending on the actions of the 1<sup>st</sup> actors. Finally, the proportion of strategic choices for each of the 8 combinations was calculated and compared them to chance levels.



Table 1: Rational choices dependent on the combination of social and non-social options.

Social option	Non-social option	Strategic choice
Snowdrift	0	Social option
<i>Competitive</i>	0	Social option
Snowdrift	1	Social option
<i>competitive</i>	1	Social option
Snowdrift	3	Same action of 1 <sup>st</sup> actor
<i>competitive</i>	3	Opposite action to 1 <sup>st</sup> actor
Snowdrift	5	Non-social option
<i>competitive</i>	5	Non-social option

The inter-observer agreement for the timing of decisions by chimpanzees, based on the 20% of the data, was excellent (time to access the non-social option:  $r = 0.98$ , 0.8% of data mismatches between observers; time to access the social option:  $r = 0.98$ , 1.4% of data mismatches between observers; time to access the ropes:  $r = 0.99$ , 3% of data mismatches between observers) and for bonobos (time to access the non-social option:  $r = 0.96$ , 1.3% of data mismatches between observers; time to access the social option:  $r = 0.97$ , 1.2% of data mismatches between observers; time to access the ropes:  $r = 0.95$ , 3.5% of data mismatches between observers).

### 3.7 Results

Overall, chimpanzee and bonobo pairs obtained the rewards in 92% of trials. Both ape species behaved rationally by choosing the social option when there were no rewards available in the non-social alternative (93% of trials). As expected, the proportion of choices towards the non-social option relative to the social option also increased as the rewards in the alternative platform increased. This change was not driven solely by the number of rewards in the alternative option but also by the social condition: the switch in preference from the social to the non-social option was steeper in Snowdrift trials compared to *competitive* trials (Model 14; GLMM:  $\chi^2_1 = 9.572$ ,  $N = 2218$ ,  $p = 0.002$ ,  $CI [0.284, 2.258]$ ; Figure 15).

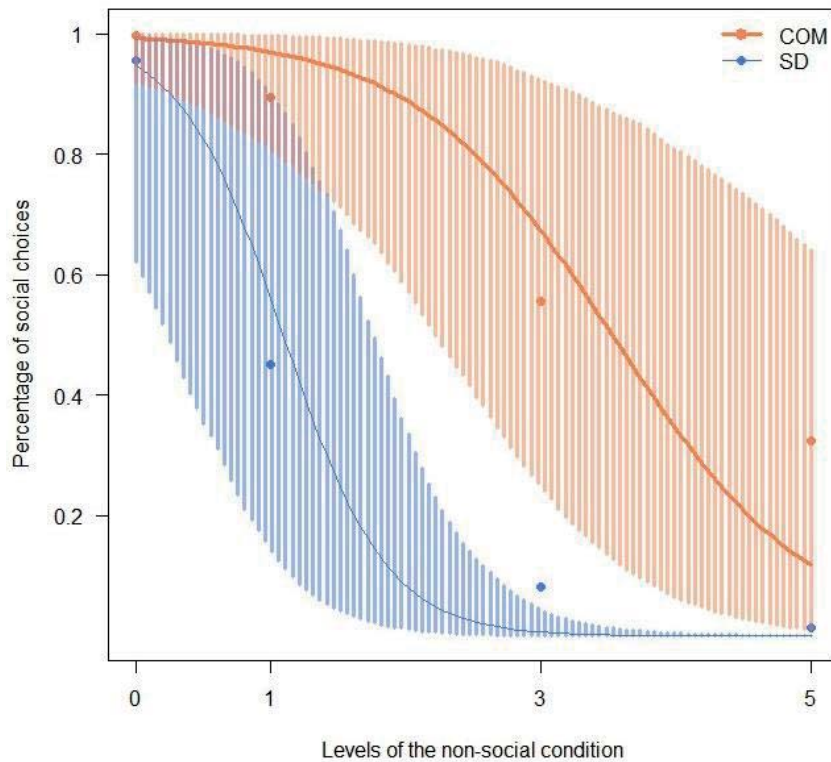


Figure 15. Percentage of the decisions towards the social choice as a function of the levels in the non-social condition and the levels of the social condition (SD and COM trials).

The first latency measure was the time taken to open the door to either platform. When there was no reward in the non-social platform apes waited longer to open the doors in Snowdrift trials compared to *competitive* trials, replicating the findings from Study 2a. However, as the rewards in the non-social platform increased, apes tended to decrease their latency to decide, and the differences between Snowdrift and *competitive* conditions decreased. This decrease in latency occurred in conjunction with a change in their decisions, from the social to the non-social option (see Figure 16 *left*; see Figure A2 with CI in the Appendices) (Model 15; LMM:  $\chi^2_1 = 6.62$ ,  $N = 2216$ ,  $p = 0.01$ ,  $CI [-0.007, 0.295]$ ). Overall, chimpanzees were faster than bonobos in both conditions (Model 15; LMM:  $\chi^2_1 = 8.06$ ,  $N = 2216$ ,  $p = 0.004$ ,  $CI [-1.061, -0.099]$ ) but there were no significant interactions between species and conditions.

The second latency measure focused on whether subjects waited further for their partner to pull in the Snowdrift condition, or whether the decision to open the door always led to immediate pulling of the rope. Both chimpanzees and bonobos did indeed wait longer to pull in Snowdrift trials compared to *competitive* trials. Additionally, as the rewards in the non-social option increased apes tended to wait longer to pull (see Figure 16 *right*; see Figure A3 with CI in the Appendices) (Model 16; LMM:  $\chi^2_1$

= 3.888,  $N = 773$ ,  $p = 0.048$ ,  $CI [-0.044, 0.37]$ ), with a more pronounced effect in bonobos. This was unexpected as at that point the content of the non-social option was already inaccessible and thus should not play a role in their decision to wait. However, these results should be interpreted cautiously as they are based on a small subset of trials (see Figure 15).

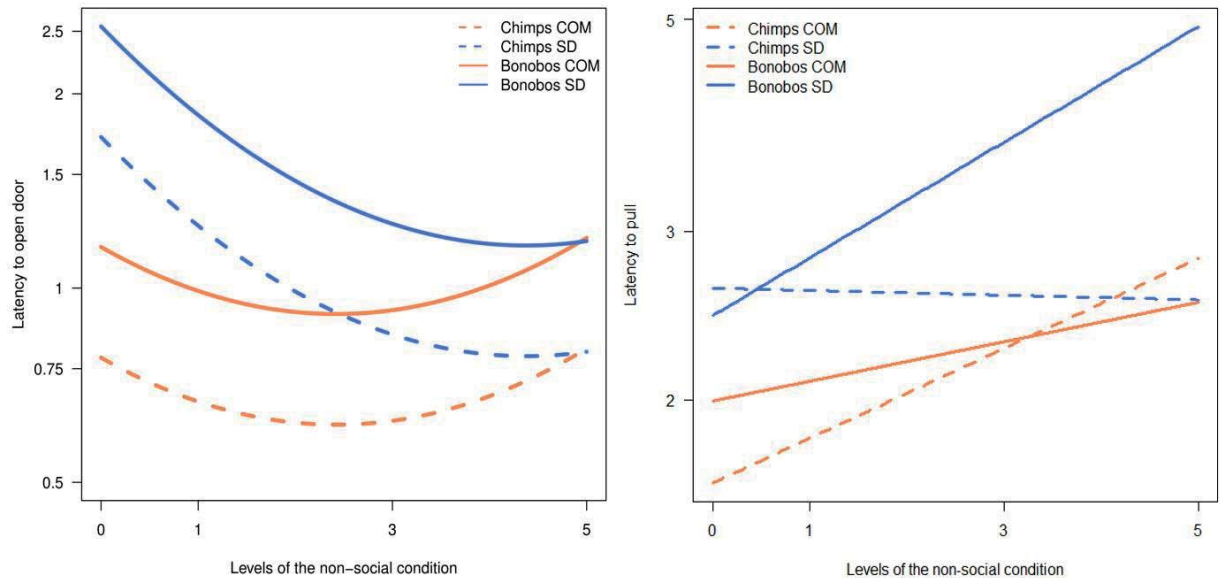


Figure 16. Latency of the subjects to open the door (left) and to pull the rope (right) as a function of the number of food pieces in the non-social option and the social option (SD and COM trials). Latencies in seconds are presented in a logarithmic scale.

Overall, individuals acting second (2<sup>nd</sup> actors) made strategic decisions on 85% of the trials. Moreover, when they could respond to the decision that the 1<sup>st</sup> actors had made in that trial –in non-social option 3, they made strategic choices on 75% of trials. However, they only chose significantly above chance when there were 0 or 5 food rewards baited in the alternative platform (pair-wise comparisons derived from Model 17: Non-social option 0-Snowdrift:  $p = 0.008$ ; Non-social option 0-competitive:  $p = 0.003$ ; Non-social option 1-Snowdrift:  $p = 0.967$ ; Non-social option 1- competitive:  $p = 0.257$ ; Non-social option 3-Snowdrift:  $p = 0.224$ ; Non-social option 3- competitive:  $p = 0.182$ ; Non-social option 5-Snowdrift:  $p = 0.003$ ; Non-social option 5- competitive:  $p = 0.02$ ; Figure 17). See the Appendices for further details of model construction and model results.

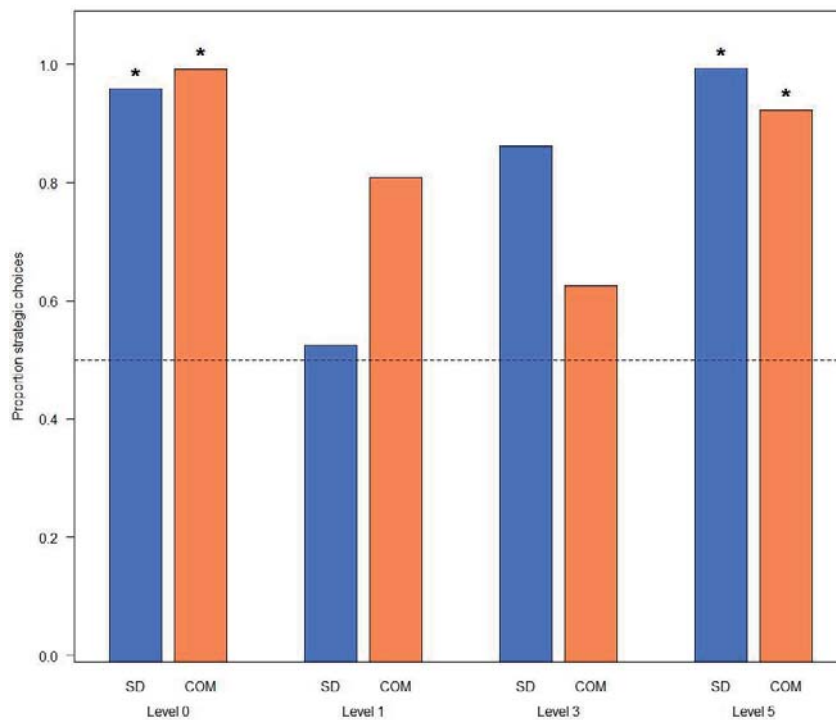


Figure 17. Proportion of strategic choices of 2<sup>nd</sup> actors across the 8 combinations of social and non-social options.

### Discussion

Results of Study 3 substantially clarified those from Study 2a by showing that when apes had access to an alternative option, their decisions were clearly strategic. They understood the payoffs of the game and acted rationally according to all the rewards involved by maximizing their benefits, as shown in previous social dilemmas (Jensen, Call & Tomasello, 2007). This may have simply been due to increased experience, as all individuals completed Study 2a before Study 3. However, if this were the case, changes across sessions in Study 2a would have been expected. Perhaps, one important factor is that the inhibitory demands of Study 2a were higher. Subjects faced the decision to either act on the apparatus (pull) or not at all, but in Study 3 apes could decide between the two actions (sliding the door left or right). Thus, one possible way to interpret these results is that when apes had to actively decide between different alternatives, it may have been easier for them to inhibit and compare their potential options and act appropriately according to the payoffs of the game in order to maximize their rewards.

### 3.8 General Discussion

Using the Snowdrift game to investigate how pairs of children, chimpanzees and bonobos coordinate their actions to overcome conflicts of interest, all three species were found to coordinate their actions effectively and succeeded in over 90% of the trials. All species showed clear indications of strategic decision-making, trying to maximize their own rewards while maintaining high levels of coordination. In Study 2b, children's communicative acts revealed clear signs of strategic behaviour but no such indication was observed among apes. In Study 3, in which apes had access to an alternative (non-social) option, their decisions were clearly strategic even though communication between partners was still virtually nonexistent.

Children are skilled at coordinating for mutual gain from a young age (Brownell et al., 2006; Duguid et al., 2014; Grueneisen & Tomasello, 2016; Warneken et al., 2014; Wyman et al., 2013) Even in situations where the risk of coordination failure is increased, children are able to use communication and theory of mind reasoning to avoid this risk (Duguid et al., 2014; Grueneisen & Tomasello, 2016; Grueneisen et al., 2015; Wyman et al., 2013). However, the goals of partners in those studies were aligned (i.e., there was no conflict of interest between partners). The current study showed that even when facing with a potential conflict of interest, children's rate of coordination failure was very low. Crucially, their success in the task cannot be attributed to a failure to appreciate the conflict of interest because their communicative exchanges indicated that they encouraged their partners to pay the higher cost to maximize their own rewards.

The results of this study are consistent with Grueneisen and Tomasello (2016) who also observed high levels of coordination in five-year old children playing a version of the Snowdrift dilemma. Coordination in that study was maintained by turn-taking, which also has been shown to enable resource sharing in a collaborative task (Melis et al., 2016). Note however, that children in those studies always depended on their partner to obtain either the preferred reward (Grueneisen & Tomasello, 2016) or all the rewards (Melis et al., 2016). In contrast, the procedure used in this study eliminated a strict partner dependency because Snowdrift trials were randomly intermixed with *competitive* trials in which children competed to obtain the preferred reward by pulling first, without the need of their partner's action. Besides preventing partner dependency, mixing Snowdrift and *competitive* trials may have made a turn-taking strategy much more cognitively demanding than previous studies—and therefore useless—because it would have required children to keep track of all their previous actions and outcomes to maximize efficiency. However, a consequence of this strategy is that the coordination was maintained despite a skewed reward distribution between

partners —also observed in Grueneisen and Tomasello (2016), perhaps because receiving some reward was more important than the social comparison, but further research is needed to determine the effects of resource inequality on coordination.

Apes also solved the Snowdrift dilemma successfully (coordination in 98% of the trials) but their behaviour differed from children's in two important ways: there was little communication between partners and only one partner pulled in most pairs. This strategy produced an equal distribution of rewards between partners, which may seem surprising given that apes behaved as rational maximizers in other studies (Bullinger et al., 2011b; Jensen et al., 2007). However, the observed equal distribution may have been a by-product of the “one-partner-pulling” strategy combined with the counterbalancing of payoffs across multiple trials. Even when one of the partners was a passive participant (always waiting) it does not necessarily mean that they were indifferent to the outcomes. Apes experienced pulling in both conditions during the training and experimental sessions, and there is evidence suggesting that subordinate chimpanzees wait to pull a rope to “negotiate” a better reward distribution with a dominant individual (Melis et al., 2009). Thus, it is conceivable that some apes preferred to obtain lower rewards instead of competing for higher rewards to avoid conflict (Chalmeau, 1994). However, in the current study it is difficult to ascertain whether not pulling was a strategic decision, or some individuals were content with the food received for not pulling at all.

Study 3 directly addressed this ambiguity by offering an alternative option to inaction. Based on their change in preference from social to non-social choices (and their associated timing), apes generally behaved more strategically in Study 3 than in Study 2a. However, apes not always maximized their rewards in all conditions. For instance, when apes were confronted with the *competitive* condition (five pieces of food in the roped end) and the alternative option was baited with three pieces of food, they sometimes preferred the lower but secure reward even when they acted first (20% of times they chose the non-social option). Perhaps an aversion to either risk or even competition with their partners led them to select lower value (but secure) rewards in those cases. In the absence of risk, chimpanzees prefer to act alone rather than to collaborate provided both actions yield the same rewards (Bullinger et al., 2011b) but they switch to collaborative options that result in better outcomes than acting alone. However, if social risks increase, as in the current study or other tasks (Duguid et al., 2014), they may prefer lower but more secure rewards, thus managing a trade-off between competition and reward maximization.

Based on previous findings (Haun et al., 2011; Heilbronner et al., 2008) bonobos were expected to be more risk averse (preferring the secure option) than chimpanzees but no clear inter-specific differences were found. A possible explanation for this result is that most studies have focused on

non-social risk effects. Interestingly, in a study in which bonobos could choose between feeding alone or co-feeding with strangers, they preferred the social option (Tan & Hare, 2013) despite the potential social risks involved. Thus, further studies comparing chimpanzees and bonobos across different social and non-social risk tasks are needed to fully understand possible differences between these two species.

Finally, it was investigated whether apes took advantage of situations in which they already had information about their partner's decisions (i.e., when their partner acted before them). Overall, individuals acting second chose strategically. However, in those conditions where the strategic choice of 2<sup>nd</sup> actors differed depending on what their partner had chosen in that trial, they did not perform significantly above chance. The findings of this study are consistent with previous studies in competitive contexts showing that chimpanzees can adjust their strategies in anticipation of likely decisions of partners (Kaminski, Call & Tomasello, 2008; Schmelz, Call & Tomasello, 2011) but no clear strategic responses to a partner's specific decision were found. The short time that apes had to respond to their partner and the random presentation of conditions within sessions may have contributed to this outcome. Apes anticipated their partner's likely behaviour when they faced a symmetrical conflict of interest in which both participants started with the same probabilities to maximize their payoffs. However, to explore in more detail whether apes act strategically in response to their partners' decisions, future research could focus on how apes solve conflicts of interest when only one individual has bargaining leverage (i.e., only one member of the pair has access to an alternative option).

In conclusion, using a Snowdrift game to model situations such as group hunting or agonistic intergroup encounters in which individuals need to overcome a conflict of interest to coordinate with others, it was found that pairs of children, chimpanzees and bonobos successfully solved this social dilemma. However, they did so in different ways. Whereas both partners pulled and communicated in children, one of the partners did most of the pulling in apes with virtually no communication. Nevertheless, an additional study that included an additional secure option revealed that apes behaved strategically by choosing options that maximized their own payoffs, which in some cases included delaying (or accelerating) their choices to net the largest reward available.





# CHIMPANZEES AND CHILDREN COOPERATE IN A PRISONER'S DILEMMA

## *4.1 Introduction*

Cooperation is a widespread phenomenon in nature. From unicellular organisms to human societies, evolutionary complexity can only be explained through cooperative processes in which biological entities work together to achieve common benefits (Maynard-Smith and Szathmary, 1997). Sometimes cooperation is the best strategy for all agents (Boucher, 1988; Clutton-Brock, 2009) but in other occasions cooperation comes together with the possibility to defect and reap the benefits from the cooperative acts of others. This tension between cooperation and defection is best captured in the Prisoner's Dilemma model (Rapoport & Chammah, 1965; Tucker, 1950). In this model two players can either cooperate or defect. Mutual cooperation is always better than mutual defection. However, for a single player it is always better to defect regardless of the other player's decision, leading to mutual defection if both play rational. In this situation, thus, cooperation cannot thrive (Dawkins, 1976). Yet, cooperation has evolved. Therefore, to solve this conundrum, the Prisoner's Dilemma has been widely used to study the conditions in which human cooperation could have evolved, bridging experimental research (Sally, 1995; Wedekind & Milinski, 1996) and agent-based modelling (Axelrod, & Hamilton, 1981; Nowak & Sigmund, 1994). Moreover, its use has also been extended to investigate animal cooperation (Dugatkin, 1988; Stephens, McLinn & Stevens, 2002; Wilkinson, 1984; Wood, Kim & Li, 2016).

Besides its importance as a model to study the evolution of cooperation, the Prisoner's Dilemma also provides a promising framework to explore in detail the decision-making strategies that social animals require to resolve situations of conflict. From a comparative perspective it is of special interest for us to compare the strategies of our closest living relatives, the chimpanzees, with those of children in a Prisoner's Dilemma scenario. This approach, in line with previous studies exploring the strategic abilities of chimpanzees and children to coordinate in other cooperative games (Duguid et al., 2014; Studies 2a and 2b in Chapter 2), contributes to understand the evolutionary roots of human cooperation and decision-making.

From the literature, the general picture states that humans tend to cooperate during Prisoner's Dilemma interactions and thus, deviate from the rational assumptions of the game (i.e., mutual defection)<sup>4</sup>. In fact, people cooperate more than expected in a wide range of Prisoner's Dilemma versions including one-shot interactions (Cooper, DeJong, Forsythe & Ross, 1996; Engel & Rand, 2014; Kiyonari et al., 2000) and iterated presentations of the dilemma (Cooper et al., 1996; Camerer, 2003; see Rand & Nowak, 2013 for a review) in which people increase their likelihood to cooperate when the probability of future interaction is high (Dal Bó & Fréchette, 2011). This is in line with results in other non-cooperative models such as the Dictator and the Ultimatum Game. In those studies, people generally depart from the rational assumptions of the game; humans tend to behave altruistically towards others (Camerer, 2003; Henrich et al., 2001; but see Smith and Silberberg, 2010).

From a very young age, human children already possess uniquely human cooperative motivations to help and share with others (Brownell et al., 2013; Liskowski et al., 2006; Warneken & Tomasello, 2006). Moreover, from a young age children tend to deviate from the rational assumptions of social games such as the Ultimatum (Murnighan & Saxon, 1998) and the Dictator Game (Benenson, Pascoe & Radmore, 2007), displaying altruistic behaviour in line with adult studies. However, little is known about young children strategies in the context of the Prisoner's Dilemma. In a previous study, Matsumoto and colleagues (Matsumoto, Han, Yabrove, Theodoru & Carney, 1986) investigated four-year old children behaviour when they were presented with a simplified version of the Prisoner's Dilemma. In that task, pairs of children had to choose between competition or cooperation cards to place on a board. The result of their choices determined whether they would obtain pennies or not; according to one of the four possible outcomes of the Prisoner's Dilemma payoff matrix. They found that children increased their moral solutions across sessions (a moral solution was defined as both children choosing to cooperate) and that the degree of friendship was positively related with their moral acts. However, in that task children were encouraged to discuss their strategies and express their thoughts and feelings; such actions thus, could have enhanced children strategic decision-making. A more recent study by Blake and colleagues (Blake, Rand, Tingley & Warneken, 2015) presented 10- and 11-year old children with an anonymous Prisoner's Dilemma game. They found that children cooperated more often in iterated versions of the dilemma compared to one-shot interactions. Anonymous context (i.e., when people cannot see or hear each other and they do not meet before the onset of the game) may be useful to control for factors such as reputation. Yet, this approach prevents a complete comparison between humans and apes. First, anonymous context are not common in young children and apes social interactions; the latter, in fact, live in the same social

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<sup>4</sup> Mutual defection is the rational strategy unless the game is played in an infinite amount of rounds (Friedman, 1971).

groups and it is very complicated to test them with strangers. Second, it is difficult to determine whether apes and young children understand that they interact with a conspecific in an anonymous context.

Unlike children, chimpanzees have never been tested in a Prisoner's Dilemma. However, results from other social studies have found that, overall, chimpanzees behave rationally to maximize their benefits regardless of others (see Jensen, 2016 for an extended review on apes prosociality; but see Engelmann and Herrmann, 2016). For instance, in non-cooperative games such as the Ultimatum game chimpanzees do not show other regarding preferences. In this game, both proposers and receivers try to maximize their rewards whenever possible: proposers keep the highest share for themselves and receivers, in turn, accept any share (Jensen et al., 2007, but see Milinski, 2013; Proctor, Williamson, De Waal & Brosnan, 2013). In cooperative scenarios such as the Stag Hunt, chimpanzees seem to coordinate for mutual benefit to increase their outcomes (Bullinger et al., 2011a; Duguid et al., 2014). When conflicts of interest are involved but cooperation is still necessary to reap benefits, chimpanzees can negotiate unequal reward distributions (Melis et al., 2009). Moreover, our previous findings suggest that chimpanzees and bonobos cooperate in different versions of the Snowdrift game (Studies 1 and 2a in Chapter 1 and 2). In the Snowdrift, in contrast to the Prisoner's Dilemma, unilateral cooperation is better than defection provided that the partner defects. Thus, would chimpanzees and children, coordinate their actions in scenarios where unilateral cooperation is not beneficial for cooperators?

To answer this question we presented pairs of both species with a conflict of interest in the form of a Prisoner's Dilemma with two conditions: a Prisoner's Dilemma and a *competitive* condition. In the Prisoner's Dilemma, the best strategy was to wait for a partner to pull and thus obtain all the rewards (2 grapes for chimpanzees and 2 glass marbles for children). The second best strategy was to coordinate with the partner and pull together to divide the rewards<sup>5</sup>. The worse strategy was to pull and send all the potential rewards to the partner. Finally, if both subjects defected they would lose the possibility to obtain any reward after a short period of time. We compared Prisoner's Dilemma to *competitive* trials, in which subjects were required to pull faster than their partner to obtain all the rewards. In *competitive* trials pairs of chimpanzees and children could also pull together and divide the rewards as in Prisoner's Dilemma trials.

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<sup>5</sup> Unlike in the standard version of the Prisoner's Dilemma, in this task mutual cooperation is not incentivized. This change was not possible due to the apparatus contingencies —the food was baited all at once and thus all four possible outcomes stemmed from the initial distribution. Therefore, both collaboration and reciprocity led to the same rewards over time.

If subjects behave strategically, we expect higher pulling rates together with higher success in *competitive* trials, and higher latencies to pull in Prisoner's Dilemma trials for both species. Moreover, we anticipate the frequency of coordination trials (i.e., trials in which individuals pull together and divide the rewards) to increase with experience in both conditions (i.e., within trials). Finally, based on previous studies (Duguid et al., 2014; Studies 2a and 2b in Chapter 2), we expected verbal communication to play a role in children strategies to overcome the conflict of interests presented, communicating more often during Prisoner's Dilemma interaction when they require of their partners actions to obtain rewards.

## 4.2 Material and Methods: Study 4a

### Subjects

We tested 14 captive chimpanzees (7 males;  $M_{age} = 21.1$  years; see Table A17 in the Appendices for more information) housed at the Wolfgang Köhler Primate Research Center in Leipzig zoo. During the first test phase of the study, the chimpanzees made up 7 unique pairs. After phase one, ten chimpanzees completed four cooperative training sessions with a human experimenter before they were tested again with the same partner for the second test phase. The remaining four subjects could not participate in the training sessions and in the second phase of the study as two of them moved to another zoo.

### Materials

We presented pairs of chimpanzee with a rectangular tray (91x10 cm) placed between the two subjects (Figure 16). A rope was connected at either end of the tray so that each subject could pull from one of the ropes' ends. The tray was baited with a grape at each end side. The tray could be placed either at the bottom (Prisoner's Dilemma condition) or at the top position (*competitive* condition). If one ape pulled in the Prisoner's Dilemma condition, both grapes would roll down to its partner side (Figure 18a). In contrast, if one ape pulled in the *competitive* condition, the grapes would roll down to its own side (Figure 18b). Therefore, a pulling act during Prisoner's Dilemma trials was defined as *cooperation* while pulling in *competitive* trials was defined as *competition*. At the same time, no pulling in Prisoner's Dilemma trials was defined as *defection*. Alternatively, in both conditions

chimpanzees could coordinate their actions to pull from their ropes simultaneously and divide the rewards (Figure 18c).

The end sides of the tray sat on two elevators. Each elevator was inserted in a vertical tower made of Plexiglas (65 cm high). The elevators could keep the tray at the bottom or at the top position (Prisoner's Dilemma or *competitive* condition respectively). To maintain the elevators and the tray at the top position we used counterweights —metal cylinders of 0.5kg— attached to the elevators.

Each tower was attached to one of the subjects' rooms through a Plexiglas mesh that prevented the apes to reach the apparatus. Each Plexiglas mesh had two openings, one at the top and another at the bottom position that could be opened by the experimenters to allow chimpanzees' access to the ends of the tray. Under the apparatus there were two ramps, each oriented towards one of the subjects' rooms.

The ropes were connected to its corresponding elevator through a system of pulleys that allowed the vertical movement of the elevators along the towers when the subjects pulled. The baited rewards could be accessed from three different locations: directly from the tray through the openings at the top or at the bottom position, or from the ramps under the apparatus.

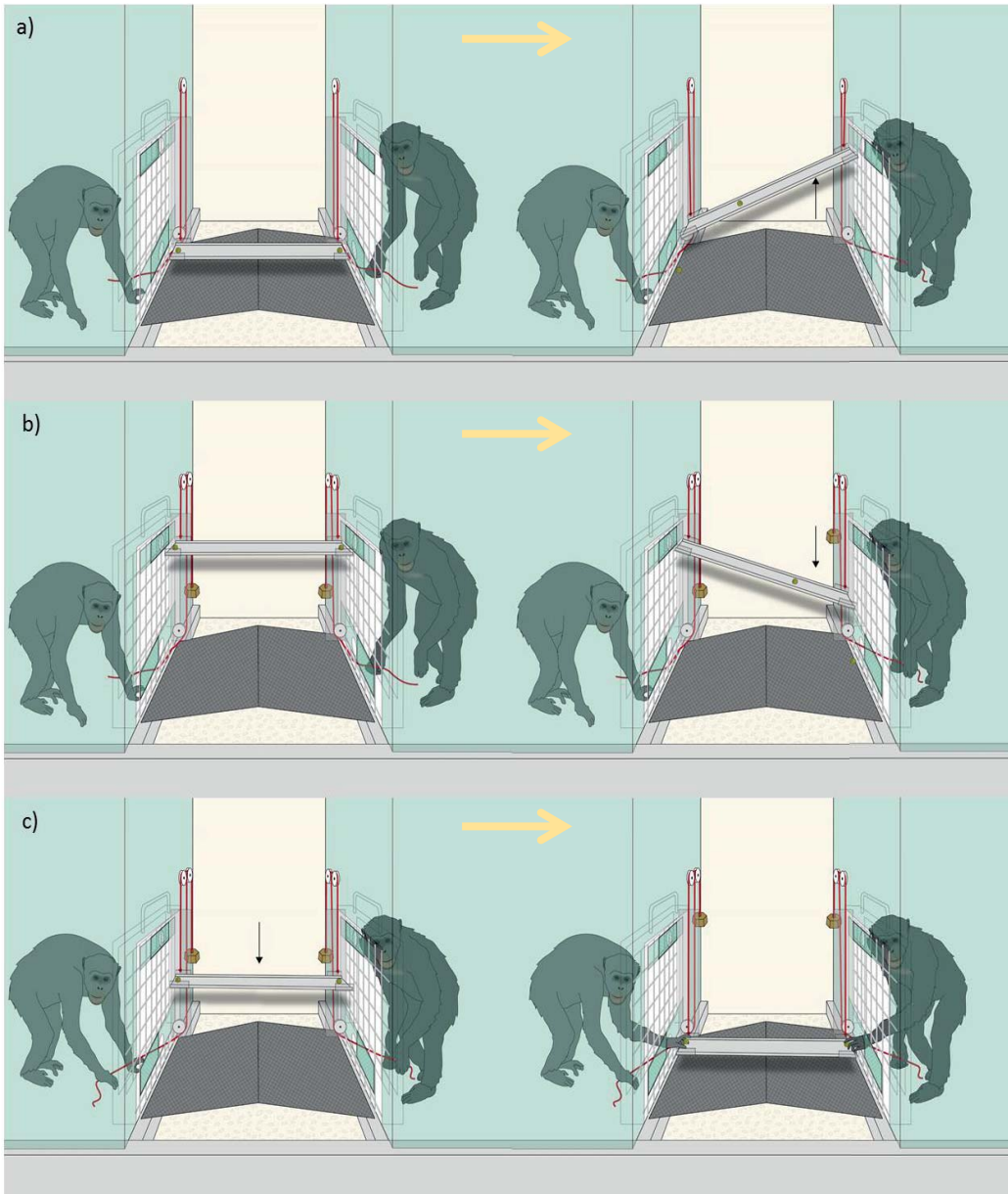


Figure 18. Experimental set-up of Study 4a. Prisoner's Dilemma condition (18a), competitive condition (18b) and collaboration example (18c)

### Procedure

Chimpanzees were tested in a within subjects design in the Prisoner's Dilemma and the *competitive* conditions. Subjects could either pull (cooperate and lose) or do nothing (defect and win) in Prisoner's Dilemma trials, and pull (compete and win) or do nothing (lose) during *competitive* trials. If only one individual acted, the rewards would be collected from the ramps under the tray. If both individuals coordinated during Prisoner's Dilemma trials (tray at the bottom position), they would lift the tray from the bottom position and obtain the grapes through the top openings. In contrast, in *competitive*

trials (tray at the top position) chimpanzees would pull down the tray from the top position to obtain the grapes through the bottom openings.

At the start of a test session, one experimenter opened either the top openings during Prisoner's Dilemma trials or the bottom openings during *competitive* trials. At the start of a trial, two experimenters baited the grapes at the ends of the tray. The subjects had 15 seconds to act. After this time, an experimenter would remove all the rewards left on the tray.

### *Individual training*

This training phase served to show the apes the payoff contingencies of the task and how to access the rewards. During this training phase the door connecting both rooms remained open. Each subject was required to complete two individual sessions on separate days. Within each session subjects experienced four trials, one trial per condition from each side of the apparatus. Trials were randomly presented within sessions. On a given trial, a subject had to pull to obtain the grapes either from the ramp oriented towards its room (in *competitive* trials; tray at the top position) or from the ramp oriented towards the opposite room (in Prisoner's Dilemma trials; tray at the bottom position).

### *Social training*

In this training phase we demonstrated that, depending on the condition, chimpanzees could either get or lose the rewards by either pulling themselves or by waiting for a human partner to pull. Therefore, apes experienced four possible outcomes: obtain all the rewards by pulling in the *competitive* condition, obtain no rewards by pulling in the Prisoner's Dilemma condition, obtain no rewards by waiting in the *competitive* condition and obtain all the rewards by waiting in the Prisoner's Dilemma condition.

Each subject was required to complete four sessions with the human partner on separate days, changing sides between sessions. There were eight trials per session. In each half of the session there were two trials per condition presented in a randomised order. The subject and the human partner switched roles after the fourth trial so that in half of the trials chimpanzees had access to their rope and in the other half only the human stooge had access to their rope (the human stooge had always access to the rope but only pulled in half of trials). This manipulation was necessary to prevent chimpanzees from pulling and to let them experience all possible outcomes.

Additionally, there were two sessions in which chimpanzees could retrieve the rewards directly from the tray through the openings in the Plexiglas mesh. This training had the purpose to show the apes that they could also retrieve the rewards from the openings (in previous training sessions they only retrieved the rewards from the ramps). These two sessions were presented after the second and the fourth social training session. As in the individual training, chimpanzees were tested alone and the door connecting both rooms remained open. Each session contained four trials, one per condition from each side of the apparatus. Trials were randomly presented within sessions. In these trials, either the top openings during *competitive* trials or the bottom openings during Prisoner's Dilemma trials were already accessible to the chimpanzees. Chimpanzees did not have access to the ropes during these two sessions.

### *Coordination training*

After the first test phase, each chimpanzee performed four coordination training sessions with a human experimenter. The purpose of these sessions was to show chimpanzees that they could mutually coordinate their actions with their partner and divide the rewards —by accessing the rewards through the Plexiglas openings after pulling together with the human experimenter. To do so, we placed each grape inside a transparent dish attached to each end of the tray so that the grapes did not roll down when the tray was slightly inclined. Each session consisted of four trials per condition, randomly presented within sessions. The subject and the human switched sides between sessions.

### *Test sessions*

After the social training, we paired chimpanzees in the test sessions. Each pair performed 16 test sessions divided in two test phases of eight sessions. Each phase contained four sessions per condition presented in blocks. Pairs were divided in to two groups so that half started with the four Prisoner's Dilemma sessions and the other half with the four *competitive* sessions. Each session contained 8 test trials. In contrast to the training sessions, during test sessions each chimpanzee had constant access to its own rope end. In Prisoner's Dilemma sessions the top openings remained open while the bottom openings were open during *competitive* sessions. Subjects switched sides between sessions. After the cooperation training, each pair was tested for another eight test sessions (test phase 2). Chimpanzee pairs started the second test phase with the condition they finished the first test phase.



### Coding

We scored five dependent measures: efficiency, latency to pull, pulling rates (including individual strategies derived from individual pulling rates), whether chimpanzees coordinated their actions within trials, and the length of coordination trials. We defined efficiency as the proportion of trials in which at least one member of a pair was successful —retrieving at least one grape. Latency was the elapsed time between the moment the experimenters baited the grapes on the tray until the first pulling action occurred. A pulling action was the first movement of either end of the tray. Coordination trials were defined as trials in which chimpanzees pulled together and split their rewards. Finally, the length of those trials was the elapsed time between the first movement of the tray until the last tray end sat horizontally at the bottom level (this was only coded for the *competitive* condition because coordination did not occur in the Prisoner's Dilemma condition).

From the pulling rates —regardless of the rewards' distribution— we calculated their proportion of strategic decisions: the proportion of times they competed in *competitive* trials and the proportion of times they defected in Prisoner's Dilemma trials. Based on the information scored, we classified subjects in three qualitative categories: *pullers* pulling in at least 75% of trials in both conditions, *non-pullers* pulling in 25% or less of the trials in both conditions and *strategisers* as subjects that obtained rewards at rates significantly above chance in both conditions (by competing in *competitive* and defecting in Prisoner's Dilemma conditions).

The inter-observer reliability was excellent based on the 20% of the data on chimpanzees' pulling rates (Cohen's Kappa = 0.88). To calculate the inter-observer agreement for the timing of decisions, we only counted the trials in which both observers scored a pulling action. The inter-observer reliability based on the 20% of the data on latencies was excellent ( $r = 0.99$ ).

## 4.3 Results

Overall, pairs obtained the rewards in 89% of trials (either one or two grapes) and at least one partner pulled in 95% of trials. All unsuccessful trials (11%) in which no pair member pulled (5%) or pulled but failed to retrieve any reward (6%), occurred in the Prisoner's Dilemma condition. We found that chimpanzees were more likely to wait in Prisoner's Dilemma trials compared to *competitive* trials and these differences increased across sessions (Model 18; GLMM:  $\chi^2_1 = 7.61$ ,  $N = 720$ ,  $p = 0.005$ ,  $CI [-5.35, 0.68]$ ; Figure 19).

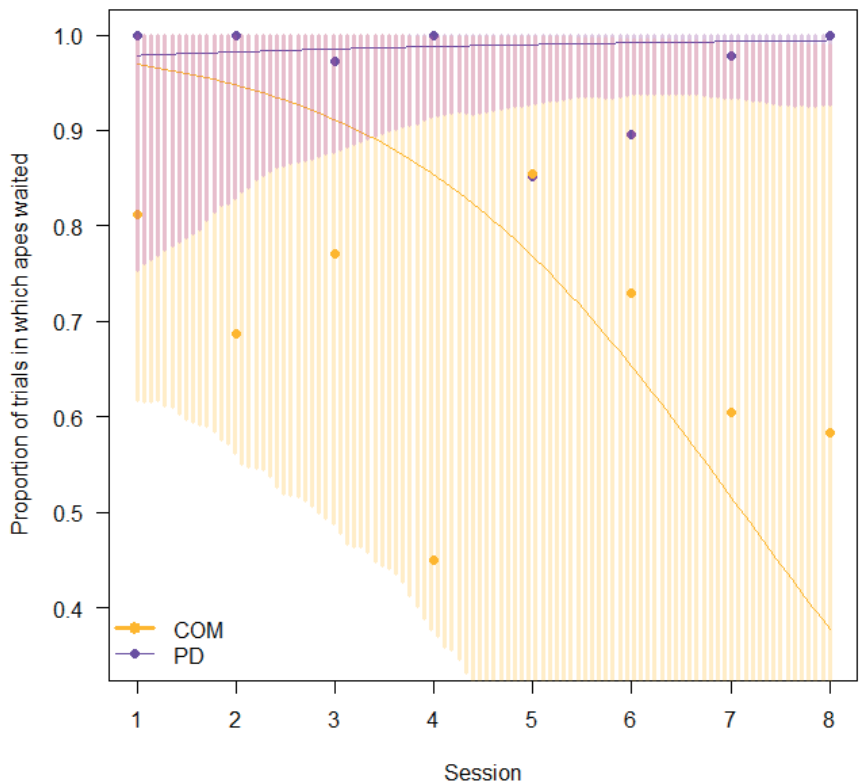


Figure 19. Proportion of trials in which chimpanzees waited for a partner to pull in Prisoner’s Dilemma (PD) and competitive (COM) trials. The lines represent the fitted model and the shadowed areas represent the CI at 95%.

Additionally, when chimpanzees did wait to pull, they waited longer in Prisoner’s Dilemma trials than in *competitive* trials and this difference also increased across sessions (Model 19; LMM:  $\chi^2_1 = 12.33$ ,  $N = 590$ ,  $p > 0.001$ , CI [-1.64, -0.45]; Figure 20 left) and trials (Model 19; LMM:  $\chi^2_1 = 12.57$ ,  $N = 590$ ,  $p > 0.001$ , CI [-0.77, -0.24]; Figure 20 right).

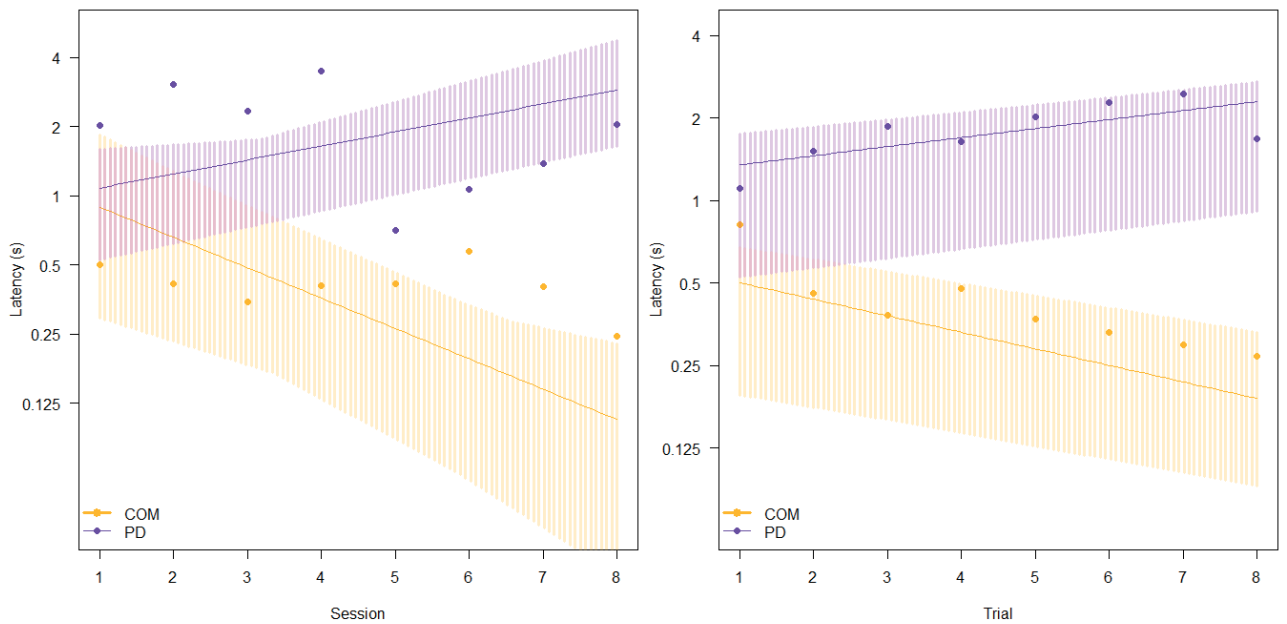


Figure 20. Latency of the 1<sup>st</sup> puller to pull the rope in PD and COM trials across sessions (left) and across trials (right). Latencies in seconds are presented in a logarithmic scale.

From their pulling rates we classified four subjects as *pullers*, none as *non-pullers* and four as *strategisers*. The remaining six were unclassified. The four *strategisers* (four male chimpanzees) pulled in *competitive* trials and not in Prisoner's Dilemma trials (binomial test,  $p < 0.005$ ). Moreover, we found a positive correlation ( $r = 0.84$ ; Figure A4 in Appendices) between the average proportion of strategic choices and the ratio of grapes obtained per trial, suggesting that *strategisers* maximized their payoffs compared to other individuals.

Overall, chimpanzees coordinated in a small amount of trials (only in 12%), mostly in *competitive* trials (see below). When chimpanzees coordinated, they did so more often in the second phase of the study, after they received the coordination training with a human experimenter (Model 20; GLMM:  $\chi^2_1 = 5.61$ ,  $N = 759$ ,  $p = 0.018$ ,  $CI [0.08, 1.81]$ ). We also found a strong trend between condition and session; chimpanzees tended to coordinate more during *competitive* trials and these tendency increased across *competitive* sessions (Model 20; GLMM  $\chi^2_1 = 3.58$ ,  $N = 759$ ,  $p = 0.058$ ,  $CI [-0.95, 40.7]$ ). The latency of coordination trials during the Prisoner's Dilemma condition was higher ( $X_{sec} = 7.27$ ,  $N = 4$ ) compared to the *competitive* trials ( $X_{sec} = 1.6$ ,  $N = 77$ ). See the Appendices for further details of model construction and model results.

## *Discussion*

Chimpanzees were able to distinguish the Prisoner's Dilemma from a purely competitive situation, adapting their strategies to maximize their rewards. Although chimpanzees tended to cooperate (unilateral cooperation, only one individual pulling) during Prisoner's Dilemma trials, they increased their latency to pull when they were presented with the dilemma —they waited longer to pull across trials and sessions. At the same time, they became faster in the *competitive* situation. This strategy was advantageous as the most strategic individuals tended to obtain higher benefits. Next, we presented the same dilemma to 5-year old children to compare their strategies to those of chimpanzees.

## *4.4 Material and Methods: Study 4b*

### *Subjects*

We tested 20 pairs of 5- to 5.5-year old children (10 pairs of boys and 10 pairs of girls) in kindergartens in the Leipzig area.

### *Materials*

In general, pairs of children were presented with the same task as chimpanzees in Study 4a (Figure 21). The apparatus was built inside a box made of wood and Plexiglas that prevented children from directly accessing the rewards (60x42x50 cm; vertical towers were 36.5 cm high). The front side of the box was opened so that Experimenter 1 (henceforth E1 and E2 for the second experimenter) could manipulate the apparatus. The box was placed on the ground between both children. Children collected glass marbles as rewards instead of food. They introduced their rewards in translucent plastic boxes. Therefore, it was hard for children to keep track of their rewards once those were inside their boxes.

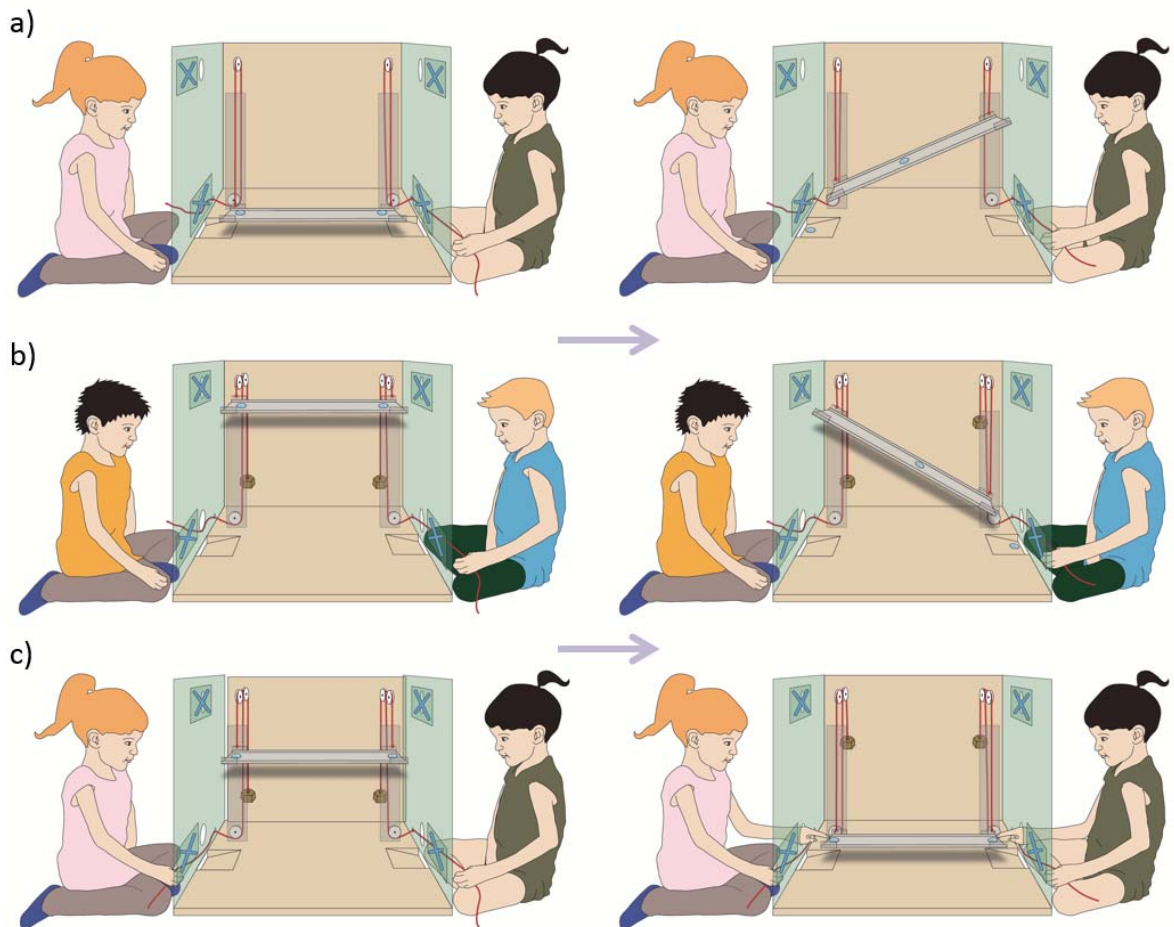


Figure 21. Experimental set-up of Study 4b. Unilateral pull in Prisoner's Dilemma condition (21a), unilateral pull in competitive condition (21b) and coordination example (21c).

### Procedure

The procedure was the same as the one presented to chimpanzees except for a few differences. Children only received two sessions compared to the 16 that chimpanzees received. Children did not conduct individual and coordination trainings in order to reduce the testing time per dyad and to prevent them to discover the collaborative solution.

At the beginning of each test session, E1 opened either the top or the bottom openings. Importantly, this time E1 opened the openings that did not allow children to directly access the rewards on the tray; bottom openings in the *competitive* session (tray at the top position) and top openings in the Prisoner's Dilemma session (tray at the bottom position). At the beginning of each trial, E1 made visual contact with each child while showing the rewards. Then E1 baited the rewards on each end side of

the tray and waited for 15 seconds approximately. After this time, E1 removed the rewards left on the tray.

### *Social training*

The social training was essentially the same as the one for chimpanzees except that children only performed one session of six trials (preceded by two pre-training trials) and they were tested in pairs with their peers; chimpanzees were tested with a human experimenter. Children swapped sides after the third trial of the session. During the social training, children collected rewards (black wooden marbles) that could be inserted in a box provided at the beginning of the training. Importantly, children did not keep those rewards for themselves after the training.

Prior to the training, E2 entered the test room with both children, showed them the apparatus and introduced them to E1. Each child took his or her position in front of the box' sides and E1 sat in front of the open side of the box. Next, E1 fed one rope through a little hole in the box so that one child could access the rope end. E2 told the child to pull. After the child pulled, E1 introduced the rope end back into the box. Then, he repeated the same procedure with the second child.

After these two pre-training trials, the social training started. The first two trials of the social training were essentially the same as the pre-training trials except that this time E1 baited one black marble at either end of the tray. At the end of each trial, E2 emphasized what the child got and showed it to the other child. After these two trials, E1 removed the access to the ropes and baited two more marbles on the tray. Right after, E1 opened either the top or the bottom accesses to the tray depending on the condition (i.e., bottom opening if children were trained in the Prisoner's Dilemma condition and top opening if they were trained in the *competitive* condition). E2 enhanced children to obtain the marbles from the tray if children did not approach the openings. With this trial children experienced they could obtain equal rewards.

After these three social training trials, children swapped sides and performed the same three trials in the other condition. This time E2 did not show children what their partner obtained, but continued to emphasise the rewards' distribution at the end of every trial. The order of conditions changed between pairs in the social training; half of them started with the Prisoner's Dilemma condition and the other half with the *competitive* one. During the two pre-training trials the tray was always located at the bottom position regardless of the condition order. In half of the pairs the child at the right side started to pull and in the other half of the pairs the child at the left side started to pull.

### *Test sessions*

After the social training each pair performed one test session per condition. Each test session consisted of eight trials and children swapped sides after completing the fourth test trial. Half of the pairs started with the Prisoner's Dilemma condition and the other half with the *competitive* condition (they started with the same condition they had previously started in the social training). Children started the first test session at the opposite side they had started the social training.

Prior to the first test session, E2 told the children that now they would play the real game while E1 showed the glass marbles —the rewards that children would collect in the following trials. Next, E2 presented children with the test boxes. E2 told them to insert the obtained marbles in their boxes and to wait for E1 to bait the marbles before pulling. After the instructions, E2 left the room. At the end of the first test session, E2 returned to the test room and told children to follow her to another side of the room while E1 reset the apparatus for the second test session. After this short pause (approximately 1-2 minutes), children took sides again at the same sides they had started the first test session. The second test session started after E2 left the room again. At the end of the second test session, every child chose 3 marbles for themselves among the collected ones.

### *Coding*

We analysed the same dependent measures as in Study 4a. Additionally, we examined whether children verbally communicated during the task, focusing on three types of communication. *Imperatives*: deontic verbs used to direct their partners' actions; *informatives*: acts aimed at informing partners about a child's current or impending actions or intentions and *protests*: statements of disapproval and objection about a partner action's or intention. Moreover, we analysed pointing towards the partner as a sign of gestural communication. For every trial, we coded whether children pairs communicated (by either one or both children) and whether each of the three categories of communication (*imperative, protests, informative*) was present within a trial (uttered by either one or both children). Communicative acts were scored from the moment E1 showed the rewards to the children until the children inserted their rewards into their boxes.

The inter-observer agreement for the timing of decisions based on the 20% of the data was excellent (pulling actions from child on the left side: Pearson's  $r=0.99$ , no data mismatches between observers; pulling actions from child on the right side: Pearson's  $r = 0.98$ , 3% of data mismatches between observers). The inter-observer reliability for communication based on the 20% of the data was very good (Cohen's Kappa =0.8).

## 4.5 Results

Children pairs obtained the rewards in 95% of trials (either one or two glass marbles). At least one child pulled in 95% of trials. From all the unsuccessful trials (5% of trials), 58% occurred in the *competitive* condition and 42% in the Prisoner's Dilemma condition. Children waited significantly longer to pull in the Prisoner's Dilemma condition ( $X_{sec} = 2.91$ ) than in the *competitive* condition ( $X_{sec} = 2.21$ ) and this difference was significant (Model 21; LMM:  $\chi^2_1 = 6.15$ ,  $N = 303$ ,  $p = 0.013$ ,  $CI [0.005, 0.69]$ ). However, unlike apes, they did not increase their latencies to pull; instead, they pulled significantly faster across sessions (Model 21; LMM:  $\chi^2_1 = 7.94$ ,  $N = 303$ ,  $p = 0.005$ ,  $CI [-0.37, -0.015]$ ) and trials (Model 21; LMM:  $\chi^2_1 = 15.59$ ,  $N = 303$ ,  $p > 0.001$ ,  $CI [-0.442, -0.142]$ ) in both conditions (Figure 22).

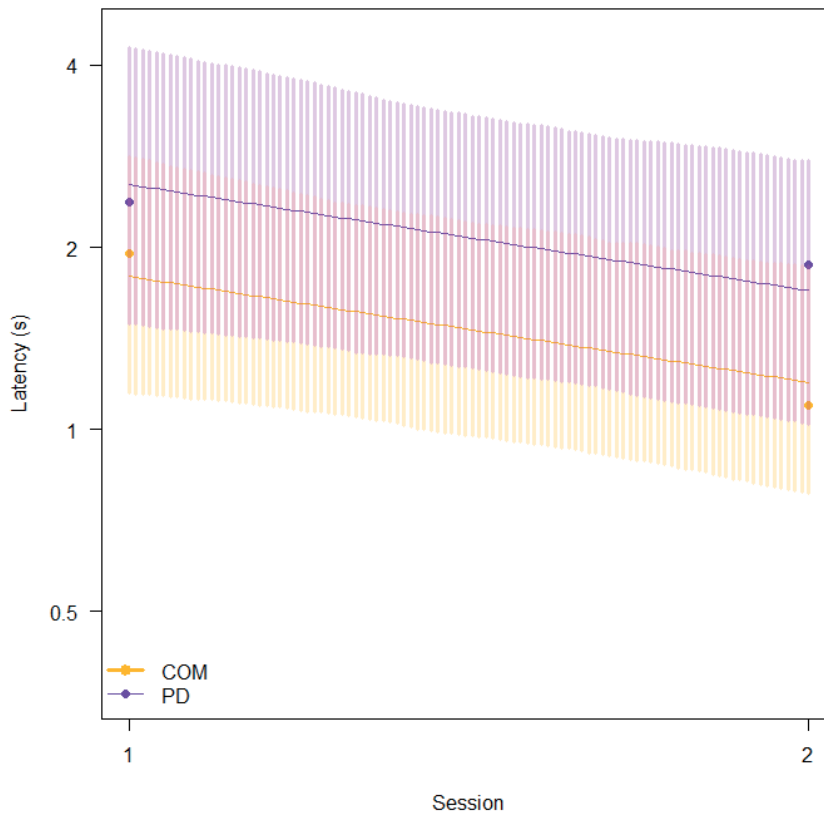


Figure 22. Latency of the 1<sup>st</sup> puller to pull the rope in PD and COM trials across sessions. Latency in seconds is presented in a logarithmic scale.

Unlike chimpanzees, children took turns to perform their pulling acts, both in the Prisoner's Dilemma and in the *competitive* condition. A turn was defined as the occurrence of a unilateral pull by individual



A preceded by a unilateral pull by individual B in the previous trial. At every trial children had a 12.5% of probabilities to reciprocate the previous action by chance (see Model 22 in the Appendix for further details). When we compared the occurrence of turns to chance levels (12.5 %) we found that children significantly used a turn-taking strategy to divide their rewards (Model 22; GLMM: Intercept: estimate = 0.22, SE = 0.56,  $p < 0.001$ ). However, they did not distinguish between conditions and did not increase their likelihood to engage in turn-taking across the study period; the full-null model comparison including the effects of condition, session and trial revealed a non-significant effect of the predictors (Model 22; GLMM:  $\chi^2_4 = 2.562$ ,  $N = 280$ ,  $p = 0.634$ ).

From their pulling rates we classified six subjects as *pullers*, none as *non-pullers* and only one as *strategiser* (binomial test,  $p < 0.005$ ). This result is in line with the finding that, overall, children took turns in both conditions. In fact, seven children pulled in half of trials across conditions. According to these results, we found a moderate positive correlation between the proportion of subject's strategic choices and the amount of marbles obtained ( $r = 0.5$ ; Figure A5 in Appendices) suggesting that children that acted more strategically obtained slightly more marbles than other children.

Overall, children coordinated in a small amount of trials (6% of trials; 50% of times on each condition). The latency of coordination trials was higher in the Prisoner's Dilemma condition was higher ( $X_{\text{sec}} = 3.66$ ,  $N = 9$ ) compared to the *competitive* condition ( $X_{\text{sec}} = 1.85$ ,  $N = 10$ ).

Children communicated about their actions in 32% of trials (in 59 Prisoner's Dilemma and 44 competitive trials out of 160 trials per condition; Figure 23). Although children communicated slightly more often during Prisoner's Dilemma trials (the situation in which they needed their partner to act in order to benefit), a full-null model comparison including the effects of condition, session and trial revealed a non-significant effect of the predictors (GLMM:  $\chi^2_4 = 8.75$ ,  $N = 320$ ,  $p = 0.068$ ). Although we were not able to analyse statistically the distribution of children communicative types, the majority of communication consisted in *imperative* and *informative* utterances (78% of the communication), occurring slightly more often during Prisoner's Dilemma trials (see Figure 23).

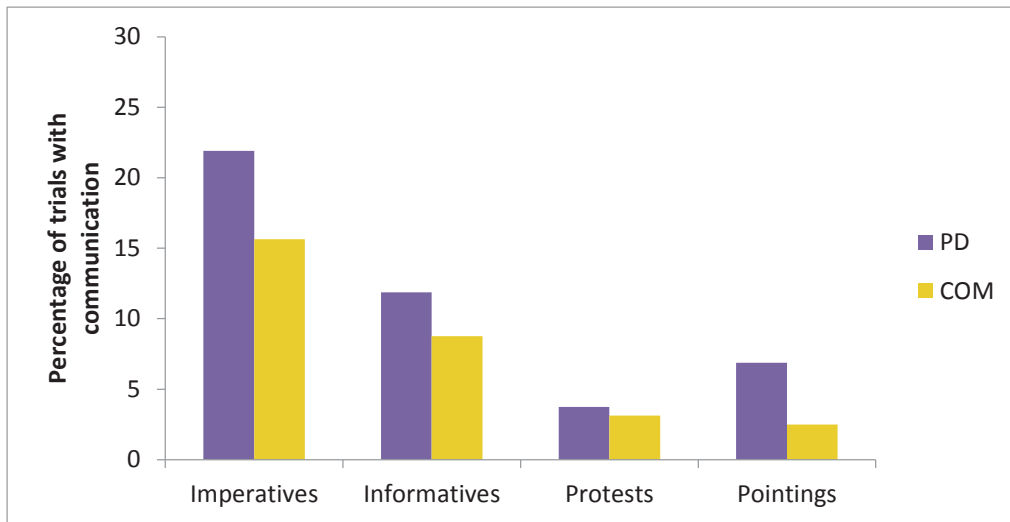


Figure 23. Percentage of trials in which every type of vocal communication and pointing occurred at least once within a trial.

In a comparison between children' and chimpanzees' strategies, the most strategic individuals were chimpanzees. This is evident from Figure 24, which shows the proportion of strategic choices in *competitive* and Prisoner's Dilemma trials. The upper right quadrant (above 50% of strategic choices in both conditions) is slightly dominated by chimpanzees. This can be explain by the fact that a majority of children took turns to retrieve the rewards, pulling around half of times in both conditions (depicted in the centre dot). See the Appendices for further details of model construction and model results.

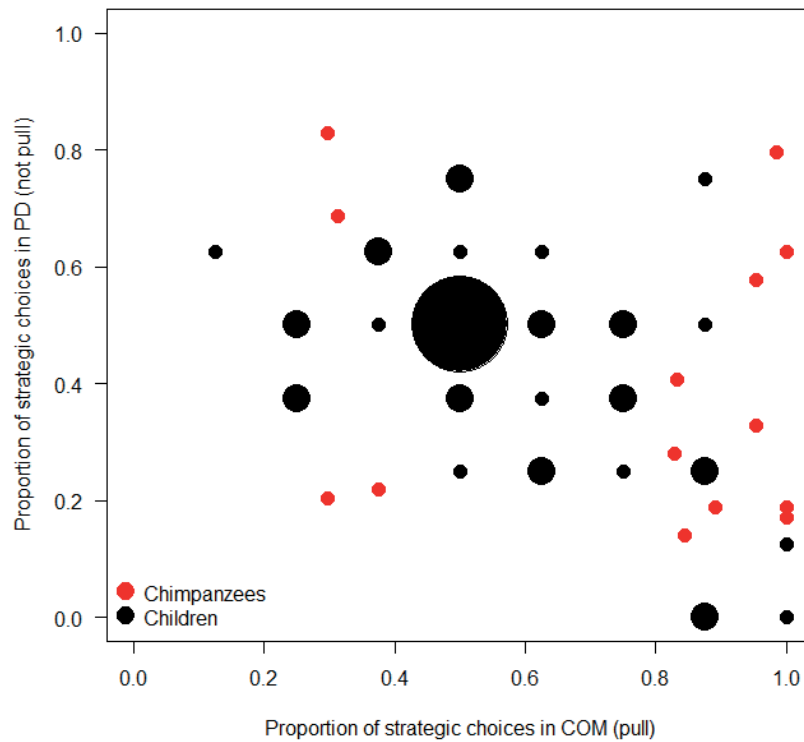


Figure 24. Proportion of strategic choices in both PD and COM trials for all subjects of the two species. The most strategic individuals in both conditions are in the top-right corner of the plot. The size of the dots represents frequencies of subjects for different scores.

### Discussion

Children actively cooperated to solve a Prisoner's Dilemma task. Similar to chimpanzees' results, they were able to distinguish both types of conditions but, unlike the apes, they established a strategy based on turn-taking to divide the rewards. Interestingly, this strategy was equally used in the Prisoner's Dilemma and the *competitive* condition. Moreover, children became faster across the study period (in both conditions), suggesting that once the turn-taking strategy was established, children did not need to wait for their partners' decisions to act. Finally, children mainly used *informatives* and *imperatives* to coordinate their actions. Surprisingly, in contrast to previous findings in the Snowdrift game (Study 2b in Chapter 2), 5-year old children did not use specific types of communication to influence their partners during Prisoner's Dilemma trials. This, however, is not surprising given the fact that children did not try to maximize their rewards during Prisoner's Dilemma trials, reflected by the general use of the turn-taking strategy.

## 4.6 General Discussion

In a study of how chimpanzees and children coordinated their actions to solve a Prisoner's Dilemma game, chimpanzees cooperated (unilateral cooperation; one individual pulling) on 79% of trials during the Prisoner's Dilemma condition and competed on 100% of *competitive* trials. Children, in contrast, were equally successful in both conditions ( $\geq 94\%$  of trials).

In line with previous studies exploring children's behaviour in a Prisoner's Dilemma (Blake et al., 2015; Matsumoto et al., 1986), in our task children cooperated to overcome a conflict of interest (mutual defection occurred in less than 6% of trials across conditions). However, large methodological differences (e.g., anonymity condition) prevent a further comparison between studies. Thus, we discuss our results in line with other studies in which children directly interact with their peers to resolve a dispute (Grueneisen & Tomasello, 2016; Melis et al., 2016; Study 2b in Chapter 2).

Children mostly achieved cooperation through turn-taking (i.e., reciprocating cooperative acts). This behavioural strategy let children sustain cooperation over long periods of time and avoid direct competitive interactions while sharing benefits. This result contrasts with children's behaviour in the Snowdrift game (Study 2b in Chapter 2). In that task, children pulled in the majority of trials in both conditions (they used a "both-partners-pull" strategy) to solve the conflict. However, a key difference between both studies is that while in the present study children were either presented with Prisoner's Dilemma or *competitive* trials within a session, in the previous study both conditions were randomly presented within a session. Therefore, a strategy based on turn-taking was unlikely to be efficient.

The result of the current study relates to previous studies showing that children tend to engage in turn-taking strategies to overcome conflicts of interest when repeatedly presented (Grueneisen & Tomasello, 2016; Melis et al., 2016). In these studies, although children preferred to take turns rather than to coordinate along a dominant asymmetry (i.e., when one individual always obtains the highest share), they could only divide their rewards through turn-taking<sup>6</sup>. In contrast, in the current study children also had the possibility to coordinate their actions to act together (collaboration) and divide the rewards in every trial. In our task, either turn-taking or mutual coordination lead to the same outcomes for both individuals. Nevertheless, mutual cooperation occurred rarely in either condition (only in 6% of the total trials). Several explanations can account for this finding. First, during training children only had experience in pulling alone. This could have hindered them to explore further

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<sup>6</sup> In Melis et al., (2016) children had to act together, but needed to take turns in order to equally split the rewards. Thus, turn-taking was the only available strategy to achieve equal shares between partners.

strategies (i.e., mutual cooperation). Second, by the age of 5-years old, children are capable of forming joint goals based on a mutual sense of "strategic trust" (Hamann, Warneken & Tomasello, 2012; Tomasello, 2016) in which both individuals understand what is better to do to achieve joint success. Thus, in this task children did not need to mutually coordinate their actions with their partners to solve the task if they mutually trusted each other as good reciprocators. Moreover, in line with recent findings in adults (Cohen, Wildschut & Insko, 2010), verbal communication could contribute to enhance trust feelings between children. Third, when individuals act together with others to achieve shared goals, they need mechanisms to support their coordination such as sharing sensorimotor information and planning actions (Vesper et al., 2016). Thus, in our task collaboration based on mutual coordination might have been cognitively harder to implement for 5-year old children compared to a strategy based on turn-taking (although see Stevens & Hauser, 2004 for a discussion on the cognitive requirements for turn-taking). To collaborate, children would have needed to time their actions in order to coordinate. Moreover, they would have needed to maintain the horizontal position of the tray while accessing the rewards.

Although in general children applied a turn-taking strategy to cooperate in both types of conditions, they were capable of distinguishing between them. This was reflected in their latencies to pull. Children waited longer to pull in Prisoner's Dilemma trials compared to *competitive* trials. This could be interpreted as a result of their conflicting preferences: on the one hand it is possible that children preferred to increase their personal gains, but on the other hand they could have also tried to avoid direct competition and maintain long term cooperation. Alternatively, they might have had a preference for fair outcomes. Yet, besides the differing latencies to pull between conditions, children tended to decrease their latencies to pull with experience in both conditions. It is likely that with experience children better understood the contingencies of the game and thus operated the apparatus faster regardless of the condition presented. Relatedly, a turn-taking strategy could have become a focal solution through precedence in order to avoid the risk of coordination failure (Schielling, 1960).

Finally, we found that children did not communicate more often during Prisoner's Dilemma compared to *competitive* trials. This might be partially explained by the fact that children treated both conditions similarly; they took turns to divide their rewards equally across conditions. This might also explain why, in general, children used similar communicative types across conditions (see Figure 23). The fact that children did not use specific types of communication during Prisoner's Dilemma trials is supported by findings showing that adults' communicative messages about their actions on a Prisoner's Dilemma do not have a strong effect on their partners' decisions (Duffy & Feltovich, 2002).

Chimpanzees were also able to distinguish the Prisoner's Dilemma from a purely competitive situation. They became more strategic with experience, waiting longer for their partners to pull by the end of the study in the Prisoner's Dilemma condition. Moreover, they became faster over time in the *competitive* condition, further implying that they learned the contingencies of the study and adapted their strategies to maximize their rewards over time.

Chimpanzees did not collaborate to solve the task and divide the benefits. In contrast, they waited for their partner to pull; the only strategy that could lead them to maximize their rewards. However, these results cannot be explained due to chimpanzees' inability to cooperate for mutual benefits: across several cooperative set-ups, chimpanzees have proven to be skilful collaborators (Duguid et al., 2014; Melis et al., 2006a) even when conflicts of interest arise or unilateral cooperation lead to rewards for both members of a pair (Melis et al., 2009; Study 1 in Chapter 1). Therefore, it is more plausible that our results could be explained in relation to other social scenarios in which chimpanzees seem to act as rational maximizers to increase their own benefits (Jensen et al., 2007; Bullinger et al., 2011). According to this idea, chimpanzees only cooperate if this strategy leads to the highest possible rewards for themselves. It is not surprising, therefore, that in our task most of the coordination occurred during *competitive* trials. This outcome likely resulted from both chimpanzees pulling at the same time in an attempt to maximize their own rewards. Thus, a selfish behaviour resulted in an indirect division of rewards. Interestingly, chimpanzees coordinated to pull together more often during the second phase of the study, after they were tested in the coordination training sessions. This training could have helped chimpanzees to better understand the contingencies of the apparatus, although it seems that it only encouraged them to pull faster in *competitive* trials, an action that indirectly resulted in higher frequencies of coordination. In fact, chimpanzees did not start to coordinate for collaboration in Prisoner's Dilemma trials after the cooperative training. In Prisoner's Dilemma trials, unlike in *competitive* trials, chimpanzees could always defect (i.e., stop pulling at any time while their partner pulls). The risk of losing all the rewards, therefore, likely explains why chimpanzees did not collaborate during Prisoner's Dilemma trials. Besides coordinating their actions to collaborate in the Prisoner's Dilemma, chimpanzees could have also solved the game by dividing their rewards through reciprocity, taking turns to pull across trials —like children did. This strategy would have led to an equal distribution of the benefits during the task and reduced competition. However, in line with previous findings (Melis et al., 2016), they did not develop any clear turn-taking strategy.

Interestingly, in this task four subjects clearly acted strategically: they pulled in *competitive* but not in Prisoner's Dilemma trials. These results together with their increasing latencies to pull across Prisoner's Dilemma trials, suggest that chimpanzees might have behaved more strategically in this

task than in the Snowdrift game (Study 2a in Chapter 2). Moreover, in the Snowdrift fewer individuals behaved strategically and most pairs solved the dilemma by applying an “only-one-partner-pulls” strategy that consisted of only one pair member pulling in both *competitive* and Snowdrift trials. These differences might be explained in relation to the nature of both games. Unilateral cooperation is worse than unilateral defection in both games. Yet, this form of cooperation is rewarded in the Snowdrift game. This difference, in turn, might have encouraged chimpanzees to behave more strategically in the Prisoner's Dilemma scenario, where the risk of ending up with zero rewards was higher.

Yet, if chimpanzees were just playing as rational maximizers in this task, we would have expected higher frequencies of mutual defection during Prisoner's Dilemma trials as a result of both subjects waiting for each other to pull. In contrast, they still cooperated in most of trials (79% of trials). Several explanations could account for these results. First, it is possible that on some occasions chimpanzees would have pulled as a way to elicit their partners to pull and benefit from the interaction. This action only cost them the effort of pulling the rope and it increased their probabilities to obtain rewards. If both individuals pulled they could turn a Prisoner's Dilemma trial into a *competitive* one: If an ape released its rope at any time, its side of the tray would return to the bottom position and, consequently, the grapes would roll down to its side. In a majority of successful Prisoner's Dilemma trials (trials where at least one individual is rewarded), only one individual pulled and the partner benefited in 70% of occasions. However, consistent with this interpretation, in the 30% of successful trials in which both individuals pulled, first pullers obtained rewards in 43% of those trials. Second, it is possible that on some occasions, chimpanzees acted prosocially towards their partners. This interpretation would be in line with results showing that chimpanzees can help partners to obtain benefits (Melis, Warneken, Jensen, Schneider, Call & Tomasello, 2011; Yamamoto, Humle & Tanaka, 2009, 2012; although see Tennie, Jensen & Call, 2016). However, this interpretation needs to be taken with caution; in previous studies chimpanzees helped partners when there was no possibility to obtain food for themselves. Moreover, in our study the two chimpanzees that obtained fewer rewards for themselves —pulling most of times in Prisoner's Dilemma trials— were paired with the two most dominant and strategic individuals. Therefore, these subjects might have just refrained from engaging in competitive interactions with dominant group members, only pulling when the dominant partner did not pull. Third, it is possible that some chimpanzees, despite understanding the contingencies of the task, could not inhibit pulling in a situation in which they had no alternative. In addition, these chimpanzees also had a long history of obtaining rewards through pulling. However, this seem unlikely as other studies have shown that chimpanzees can inhibit longer periods of time (i.e., 3 minutes) to obtain a preferred reward (Beran & Evans, 2006; Beran, Savage-Rumbaugh, Pate & Rumbaugh, 1999)

whereas in this task, trials lasted a maximum of 15 seconds. Yet, even though chimpanzees could potentially inhibit their pulls, our previous results showed that chimpanzees and bonobos were more strategic when they were given an opt-out of the social dilemma compared to a situation in which they could only pull a rope to obtain rewards (Studies 2a and 3 in Chapter 2). All in all, it is possible that a mixture of selfish (pull to influence their partner) and prosocial motives (pull for the benefit of the partner) together with individual differences (i.e., degree of inhibitory control), might underlie chimpanzees' motivations to unilaterally cooperate when such a strategy yielded no benefits for cooperators. A possible way to disentangle whether selfish or prosocial motives underlie subjects' cooperation during Prisoner's Dilemma could be to present chimpanzees with Prisoner's Dilemma trials in which only one subject can access the rope. In this situation, if only selfish motives underlie subjects' cooperation, individuals might stop pulling provided that their partner cannot pull in return.

Finally, our Prisoner's Dilemma version differs from the canonical version of the game (Blake et al., 2011; Duffy & Feltovich, 2002; Kümmerli et al., 2007) in the extent that collaboration is not incentivized—it does not provide higher shares over time compared to other strategies such as turn-taking. Children, in this scenario, came up with a cooperative strategy to reciprocate the potential rewards which provided them with the same benefits had they collaborated. Based on previous research on the Prisoner's Dilemma (Blake et al., 2011) and research showing that children prefer to collaborate rather than to act individually to obtain the same benefits (Bullinger et al., 2011), it is likely that children would have preferred to collaborate in the standard version of the Prisoner's Dilemma. However, it is an open question whether chimpanzees, acting like rational maximizers in this task, would have collaborated to increase their rewards in that scenario.

In sum, by using the Prisoner's Dilemma to further investigate chimpanzees and children's strategies to overcome conflict situations, we found significant differences between species. Children cooperated to solve the Prisoner's Dilemma and took turns to divide their rewards with their peers. Moreover, they used vocal communication to coordinate their decisions. In contrast, although chimpanzees unilaterally pulled in a majority of Prisoner's Dilemma trials, they presumably did so as an attempt to obtain rewards for themselves. In addition, chimpanzees behaved strategically to maximize their own payoffs according to the conditions presented.



## GENERAL DISCUSSION

In this dissertation I have compared the strategies that pairs of chimpanzees, bonobos and children used to coordinate their actions in situations of conflict. Overall, I found that all three species coordinated successfully, using specific strategies to overcome conflicts of interest across three different tasks based on the Snowdrift and the Prisoner's Dilemma models. The results of these comparative studies contribute to better understand human cooperation from an evolutionary perspective.

### *5.1 Great ape coordination under conflict*

A general finding stemming from the four studies conducted with apes is that chimpanzees and bonobos are capable of coordinating their decisions successfully to overcome conflicts of interest (see Table 2 for a summary of the main findings). Apes develop specific strategies to maximize their own benefits while reducing the risks of failure associated with each of the tasks presented (Studies 1 and 2a in Chapters 1 and 2). For instance, when they face an opportunity to access a secure reward (and in consequence prevent the social interaction), chimpanzees and bonobos behaved more strategically compared to a situation in which the non-social option is not present; they select either the social or the non-social option as a function of the distributed rewards and their partners' likely decisions (Study 2a and 3 in Chapter 2). Moreover, when the result of their interactions may lead to a loss of rewards (i.e., when they unilaterally cooperate in a Prisoner's Dilemma; Study 4a in Chapter 3), they behaved more strategically; they defect more and wait longer for their partners to act across the study period in comparison to situations in which they can still benefit from unilateral cooperative acts. In the next section I provide a general discussion of the thesis' findings. Subsequently, I relate these findings with previous work on apes (both experimental and field studies) and coordination in other social animals. Special attention will be paid to tasks requiring coordination when conflicts of interest are present. Finally, I consider some methodological differences between the studies reported in this dissertation in an attempt to advance future lines of research.

Table 2: Summary of great apes' studies.

Study	Main findings
Study 1	Chimpanzees collaborated to solve the task; they managed a trade-off between maintaining successful cooperation and minimizing costs.
Study 2a	Chimpanzees and bonobos waited for their partners to pull in the Snowdrift condition. A majority of dyads engaged in an “only-one-partner-pulls” strategy.
Study 3	Chimpanzees and bonobos behaved strategic when a non-social option was provided. They managed the conflict by combining information about the rewards' distribution and their partners' likely decisions.
Study 4a	Chimpanzees waited for their partners to pull in the Prisoner's Dilemma condition, and became more strategic with experience.

*Discussion of the findings*

In the first study of this dissertation (study 1 in Chapter 1), pairs of chimpanzees were presented with a conflict of interest in the form of a Snowdrift game. In that task cooperation for mutual rewards was physically costly (apes had to move a heavy weight to access the rewards). Chimpanzees preferred to collaborate even though they had the opportunity to free-ride (one ape could always pull alone and provide benefits for both partners). Through collaboration, chimpanzees reduced the costs of pulling while securing rewards. However, they also acted strategically to minimize their efforts: they waited

for their partners to start pulling and tried to pull less weight than their partners during collaborative interactions.

In the second study reported in this thesis (Study 2a in Chapter 2), pairs of chimpanzees and bonobos were presented with a different version of the Snowdrift game. In the study, chimpanzees and bonobos pairs could not collaborate within a trial but, instead, they had the possibility to reciprocate rewards over the course of the study. In contrast to the first study, cooperation was not physically costly. Instead, the conflict was presented in the form of an unequal reward distribution in an attempt to facilitate apes' comprehension of the task (differential food distributions were more conspicuous prior to the start of the trial than differential weights). Apes waited longer for their partners to pull when the conflict was presented compared to a *competitive* control condition in which it was better to pull before the partner to obtain the highest rewards. In addition, two apes behaved clearly strategic: they only pulled during competitive situations to maximize their own rewards.

Pulling simultaneously would result in direct competitive interactions as a result of each individual pulling in opposite directions, and likely losses of rewards. This reason, together with the fact that apes were always rewarded (unless both individuals refused to participate) might explain why in this task some apes developed an "only-one-partner-pulls" strategy that consisted in only one member of the pair pulling in both conditions. This strategy reduced the likelihood to compete at the cost of losing potential rewards while it secured a proportion of the rewards.

Together, the results from the first two studies of this dissertation extend the idea that chimpanzees and also bonobos are capable to coordinate their actions and cooperate despite the conflict of interest presented as long as they can obtain benefits (e.g., food rewards) from their cooperative interactions (Bullinger et al., 2011a; Duguid et al., 2014; Hirata and Fuwa, 2007; Melis et al., 2006a; 2009). In addition, the results of these two studies showed that apes would adjust their behaviour to the contingencies of each task, developing specific strategies to manage a trade-off between successful coordination and minimizing risks.

However, the resulting rewards' distribution in these two studies could also suggest that apes intentionally tried to divide rewards between partners: in the first study chimpanzees collaborated and partially divided costs between individuals while in the second study the "only-one-partner-pulls" strategy resulted in equal division of rewards between subjects. Thus, did apes tried to maximize their own rewards while minimizing risks or did they use specific strategies to divide their rewards between partners? One factor that might have played a role in apes decision-making across these tasks is the fact that apes only had one course of action available (to either pull or not). This common feature in previous studies (Studies 1 and 2a) might have covered the strategic intentions of some individuals

(i.e., consistent *pullers* and *non-pullers* in Study 2a). Therefore, to further investigate the strategic decision-making abilities of apes, I conducted a follow-up task (Study 3 in Chapter 2). Pairs of chimpanzees and bonobos were presented with the option to decide between the Snowdrift game presented in the second study (social option) and an alternative secure reward that varied between sessions (non-social option). Building on previous findings (Bullinger et al., 2011b), I found that the proportion of choices for the non-social over the social option increased as the amount of rewards in the non-social option increased. Interestingly, even though apes could obtain a higher amount of food from the tray, they sometimes refrained from taking part in the conflict (i.e., the social option) and chose the alternative secure reward instead. Moreover in this task apes did not engage in simple strategies such as the “only-one-partner-pulls”, even when such a strategy could have provided them with higher rewards on some occasions. In contrast, chimpanzees and bonobos managed the conflict by combining information about the rewards in the social and the non-social option with their partners’ likely decisions. The results suggest that the addition of the non-social alternative allowed apes to behave more strategically in comparison to previous situations in which apes actions were restricted to one choice. The follow-up study served to clarify that the strategies apes adopted during previous studies (i.e., collaboration or the “only-one-partner-pulls” strategy) were probably used as an attempt to cope with the risks involved in each task rather than as a strategy to equally distribute rewards between partners.

In a final step to investigate the decision-making strategies used by chimpanzees to coordinate in situations of conflict, I presented pairs of chimpanzees with a Prisoner’s Dilemma task (alongside *competitive* control trials; Study 4a in Chapter 3). In this task chimpanzees could either collaborate or act unilaterally to overcome the dilemma. In contrast to previous studies presented in this dissertation, unilateral cooperation led to no rewards for cooperators —the key feature of the Prisoner’s Dilemma. Interestingly, in this task chimpanzees did not develop any of the previous strategies used to solve the Snowdrift tasks; the “only-one-partner-pulls” strategy used in the second study would have resulted in no rewards for non-pullers. However, a collaborative strategy similar to the one used in the first study would have resulted in rewards for both participants over time. Yet, chimpanzees rarely collaborated in this study. It is thus possible that the difficulty to coordinate their pulls within a trial together with the risk of defection entailed in Prisoner’s Dilemma trials compared to Snowdrift trials, prevented chimpanzees from collaborating more often. In line with previous studies (Amici et al., 2014; Brosnan et al., 2009; Melis et al., 2016), chimpanzees did not develop strategies to reciprocate the rewards (i.e., turn-taking strategies). Such a strategy would have allowed chimpanzees to circumvent the social risks and overcome the Prisoner’s Dilemma while securing rewards around half of times.

Instead, chimpanzees learned to behave more strategically over the course of the study: they increased their latencies to pull across Prisoner's Dilemma trials and sessions while reducing their latencies to pull during *competitive* trials. Moreover, there were a higher proportion of strategic individuals (individuals that mainly pulled during *competitive* trials). These results contrasts with the previous Snowdrift studies (Studies 1 and 2a in Chapters 1 and 2); in those, apes waited longer to pull when the conflict was presented but did not increase their latencies over time and less apes were categorized as *strategisers*.

A possible explanation for these findings is that the higher risk of losing rewards in a Prisoner's Dilemma could have led chimpanzees to act more strategically in this scenario, becoming more hesitant to pull in an attempt to avoid losing all the rewards during Prisoner's Dilemma trials. However, as a by-product of their increased latencies to cooperate, they slightly decreased their rates of success in comparison to the previous Snowdrift studies—in some trials the experimenter had to remove the rewards from the tray. This is in line with Melis and colleagues (2009). In that study, chimpanzees had to decide to either cooperate for an equal reward distribution (e.g., two banana halves for each individual) or an unequal distribution (e.g., two bananas vs. a banana slice). They found that, despite maintaining high levels of collaboration, chimpanzees increased their latencies when they were presented with the most imbalanced situations, increasing their likelihood to fail.

Yet, despite their enhanced levels of strategic behaviour in comparison to the previous studies reported in this thesis (Studies 1 and 2a in Chapters 1 and 2), surprisingly, chimpanzees unilaterally cooperated in the majority of Prisoner's Dilemma trials. From a theoretical perspective, unilateral cooperation in a Prisoner's Dilemma is not a rational strategy. One possible explanation is that chimpanzees might have tried to entice other individuals to pull as well. While this behaviour usually resulted in unilateral cooperation—sending all the rewards to the partner, occasionally it resulted in both individuals pulling at the same time, turning Prisoner's Dilemma trials into *competitive* ones. This situation allowed chimpanzees to gain control of the situation—they could stop to pull once the partner had started, and obtained rewards more often than had they mutually defected.

### *Findings in the context of apes' experimental studies*

Chimpanzees and bonobos successfully coordinate their actions to collaborate for mutual goals (Chalmeau, 1994; Hare et al., 2007; Hirata & Fuwa, 2007; Melis et al., 2006a) even when coordination risks are high and unequal reward distributions are presented (Bullinger et al., 2011a; Duguid et al.,

2014; Melis et al., 2009). Bonobos, in contrast to chimpanzees, also collaborate for monopolizable food rewards (Melis et al., 2006b; Hare et al., 2007) due to their higher levels of tolerance (Wobber, Wrangham & Hare, 2010). A general finding, thus, suggests that apes (especially chimpanzees) seem to collaborate effectively as long as their own actions secure direct benefits for themselves, even when reward distributions are imbalanced between collaborators (Melis et al., 2009). When this is not the case (i.e. when mutual collaboration only benefits one individual), cooperation through collaboration tends to break down over time (Melis et al., 2016).

In contrast to previous research, in all the studies presented in this dissertation, apes had the opportunity to solve the conflict independently (through unilateral cooperation). Additionally, apes could overcome the conflict presented through collaboration within trials in the first and the fourth studies of the dissertation. Chimpanzees collaborated more often when they had the possibility to act alone and still obtain benefits regardless of their partners' actions (Study 1). When apes were confronted with a Prisoner's Dilemma scenario (Study 4a), in which collaboration entailed high risks of losing rewards, apes did not engage in collaboration (mutual cooperation). Instead, they acted strategically by waiting longer for their partner to pull, increasing their latencies to pull across the study period. With these results, I extend previous findings on the role of collaboration to solve situations of conflict in apes: when apes can decide whether to collaborate or free-ride but they still need to coordinate their actions, they are prone to collaborate and reduce the costs when the risks of losing rewards are minimal (Study 1 in Chapter 1). However, they prefer to act on their own when the risks of losing rewards increase (Study 4a in Chapter 3).

The opportunity to obtain rewards while free-riding might explain, for instance, why chimpanzees succeeded (i.e., at least one individual was rewarded) in a majority of trials during the Prisoner's Dilemma study (Study 4a in Chapter 3) but cooperated less often for unilateral reward distribution (i.e., when only a subject benefitted at a time) in a recent study by Melis and colleagues (2016). In that study chimpanzees were presented with two interconnected trays. Each tray was baited with one food reward. Chimpanzees could only benefit by pulling the tray towards its side of the apparatus. However, to obtain any rewards they needed to collaborate (i.e., pull the trays in the same direction); in other words, they could not obtain rewards through free-riding (i.e., waiting for their partner to pull). Chimpanzees did not succeed to overcome the conflict (i.e., they did not take turns to reciprocate and cooperation decreased across the study period); they should have foregone their short-term preferences to sustain long-term reciprocal interactions based on turn-taking. The authors argued that perhaps, chimpanzees limited skills for inhibitory control and social planning prevented apes to reciprocate rewards over time (Boysen, Bernston, Hannan & Cacciopo, 1996; Stephens & Hauser, 2004). In contrast, in the studies presented apes could free-ride and still get some rewards.

This possibility allowed chimpanzees to avoid risk situations stemming from collaboration, and in turn, behave more strategically (i.e., waiting for a partner to pull before them). Therefore, I would argue that based on the findings reported in this thesis, future research should consider in more detail apes' possibilities to free ride —either acting on their own or with the use of non-social opportunities, to avoid competitive interactions when studying apes abilities to overcome conflicts of interest. For instance, one possible avenue to explore in more detail apes strategies to overcome situations of conflict could provide individuals with bargaining leverage. For this purpose we could use the setup of Study 3. In this study each individual can decide between a social and a non-social option. To create the leverage condition we would present only one subject with the possibility to obtain rewards from the non-social option. This difference will allow us to investigate whether apes would use the rewards in the non-social option as leverage to influence their partners' decisions and whether they would understand the importance of others' leverage.

### *Findings in the context of apes' field observations*

In the field, chimpanzees and bonobos find many situations in which different subjects' interests may conflict and individuals have the possibility to coordinate in multiple ways. For instance, when they need to decide where to move next, during group defence or in situations of CAP such as cooperative hunts or group patrols. In the studies presented in this dissertation I tried to model these types of situations by presenting chimpanzees and bonobos with conflict situations in which they could always decide whether to cooperate or free-ride. Therefore, these studies allowed me to test hypothesis about apes' decision-making strategies in ecologically relevant contexts such as CAPs by focusing on their decisions and actions at the dyadic level. In the studies presented in the dissertation apes acted strategically to maximize their rewards while trying to minimize the risks contingent to each task. These results are consistent with field observations. In the context of cooperative hunts, for instance, it has been found that chimpanzees try to minimize risks when they hunt; chimpanzees are more likely to hunt when other food resources are secure (Mitani and Watts, 1999) or when estrous females are not around in order to maximize resources (Gilby, 2006). In the context of group patrols, chimpanzees are more likely to attack out-group members when they have numeric advantage and to modify their grouping and vocalizations to reduce risks of being detected in high risks areas (Wilson, Britton & Franks, 2002; Wilson, Hauser & Wrangham, 2001; Wilson & Wrangham, 2003). The finding that some individuals were willing to cooperate most times in Study 2a (i.e., the *pullers*) gives support to the hypothesis that, in the field, certain individuals, so-called *impact hunters*, are willing to initiate

cooperation during CAPs such as cooperative hunts or border patrols (Gilby et al., 2008, 2015), paying the cooperative costs (e.g., energetic expenditure, risks of injury or risks of attack) while increasing the group's overall success. Moreover, in the studies reported in this thesis chimpanzees and bonobos waited longer to act in conflict situations as a function of the conditions presented and their partners' likely decisions. This is consistent with chimpanzees' behaviour during group hunts; some individuals wait for others' to start and likely benefit by reducing their own risk of injury (e.g., avoiding male colobus defence) (Gilby et al., 2008) or by occupying better hunting spots in relation the individuals initiating the hunt (Boesch, 2002). Therefore, the findings exposed in the dissertation bridge experimental work in apes' cooperation during conflict situations with field observations of conflict resolution at the group level. Future research in both experimental and field settings should continue to investigate in more detail, for instance, the underlying motivations of *impact-hunters* to cooperate in such settings and the benefits they accrue from those interactions (i.e., whether *impact-hunters* benefit more than others or whether they behave truly altruistically for the benefit of other group members). In addition, experimental research should try to present apes with more conflicts of interest at the group level (i.e., CAPs) (Schneider et al., 2012) in an attempt to close the gap between individual decision-making at the group level and findings at the dyadic level such as the ones reported in the dissertation.

### *Findings in the context of animal cooperation*

In the last few years, the study of the cognitive abilities of social animals to coordinate for mutual benefits, has extended the initial findings that chimpanzees flexibly coordinate with their partners to obtain mutually rewards (Hirata and Fuwa, 2007; Melis et al., 2006a). Since then, diverse species including elephants (Plotnik, Lair, Suphachoksakun & De Waal, 2011), hyenas (Drea & Carter, 2009), dogs (Ostojić & Clayton, 2014), african grey parrots (Péron, Rat-Fischer, Lalot, Nagle & Bovet, 2011) and keas (Heaney, Gray & Taylor, 2017) have been tested using different versions of the pulling task design by Hirata and Fuwa (2007). The use of a general methodology allows us to compare the behaviour of a range of species and to investigate the cognitive mechanisms underlying their abilities to coordinate.

However, little is known about animal capacities to coordinate in conflict scenarios such as the Prisoner's Dilemma or the Snowdrift. In a seminal study, Stephens and colleagues (2002) tested the capacity of blue jays to cooperate in an iterated version of the Prisoner's Dilemma. In that study they found that blue jays reciprocated more often when subjects were paired with reciprocal partners



(partners that always cooperated) and when the rewards were accumulated over time (i.e., subjects could see the quantity of rewards increasing over time before they could access them). In contrast, when rewards were not accumulated—the obtained rewards were eaten at the end of the trial—and partners did not reciprocate, cooperation decreased over trials. In line with this result, a recent study by Wood and colleagues (2016) has shown that rats tested in a Prisoner’s Dilemma favoured the short-term payoffs of defection over long-term mutual cooperation. Moreover, they did not develop any Tit-for-Tat or Pavlov strategy to maintain cooperation. Although these studies use the Prisoner’s Dilemma to study animal capacities to cooperate, they differ in several aspects from our Prisoner’s Dilemma study, hindering the comparison between them. For instance, our chimpanzees lived in the same social groups while blue jays and rats were paired for the study period. Moreover, chimpanzees took their decisions in full view of their partners. In contrast, blue jays and rats actions were much more restricted; to either cooperate or defect subjects had to press a lever or hop on a perch, casting doubt whether individuals were able to understand their partners actions (in Stephens et al., (2002) this was not an option as the stooge partner always acted before the subject). Finally, in contrast to our study, in these studies active coordination (e.g., pull together to collaborate) was not required to solve the task. In all, more studies with comparable experimental designs (in the same vein of Hirata and Fuwa (2007)) are needed to provide insights into the nature of animals’ collaboration when situations of conflict arise.

So far I have provided a general discussion of the results reported in this thesis, relating them to previous work conducted with apes in experimental settings as well as to field observations and extending the discussion to other animal species. However, to fully account for the significance of the studies that compose the dissertation, in the next section I consider possible methodological differences that may help to clarify some of the results of the dissertation.

### *Methodological considerations*

In all the studies of the dissertation, pairs of apes were presented with conflict and control (*competitive*) trials. Depending on the study, they were presented either separately or intermixed within sessions. Therefore, it is possible that, instead of the conflict of interest in play, the order of trial presentation could have influenced individuals’ strategies to solve the conflict. For instance, to explain the “only-one-partner-pulls” strategy that some subjects adopted in Study 2a, the most likely explanation is that such a strategy prevented direct competition over rewards, while both subjects still obtained a share. This strategy, however, was not feasible in Study 4a; it would have resulted in

no rewards during Prisoner's Dilemma trials. Another possible interpretation is that chimpanzees used the "only-one-partner-pulls" strategy to deal with the difficulty of tracking previous reward distributions, independently of the type of conflict presented. This could explain why they only applied this strategy in Study 2a, in which Snowdrift and *competitive* trials were mixed. Therefore, future studies should carefully consider the effects of trial presentation when exploring apes' strategies to coordinate in situations of competing interests.

Due to the methodological differences between the studies that compose the dissertation it is not possible to investigate in isolation the effect of each type of risk on the apes' performance. However, based on the strategies that apes used in each task I would argue that the risks stemming from apes social interactions between partners (e.g., competitive interactions in Study 2a) could have strongly influenced the strategies apes used to deal with the conflicts presented. In Study 2a, for instance, when competitive risks were presented, a proportion of apes refused to participate (*non-pullers*). This was corroborated in Study 3 in which apes occasionally preferred the alternative option even when the social option offered them higher rewards. In contrast, chimpanzees did not stop participating in Study 4a —no subject was categorized as *non-puller*— even though unilateral pulls resulted in no rewards during Prisoner's Dilemma trials. In all, these findings suggest that apes strategies to overcome conflicts of interest are tightly influenced not just by the rewards at stake but by the social-risks contingent to the task.

## 5.2 Children's coordination under conflict

The general finding stemming from the two studies conducted with 5-year old children is that they are able to coordinate their decisions to overcome situations of conflict (see Table 3 for a summary of the main findings). Children use more sophisticated strategies to overcome the risk of failure in comparison to apes. Moreover, they use verbal communication to facilitate coordination when their interests compete. For instance, when they are presented with the opportunity to maximize their rewards by waiting for their partner to pull, they strategically wait longer and these latencies increase over the study period while securing a proportion of the potential rewards (Study 2b in Chapter 2). In contrast, when their unilateral actions lead to a loss of rewards, they develop cooperative strategies to divide the rewards (i.e., turn-taking strategy) while reducing competition (Study 4b in Chapter 3). In the following section I provide a general discussion of the findings and how the results of these two studies relate to previous research.

Table 3: Summary of children's studies.

Study	Main findings
Study 2b	Children coordinated their actions to solve a Snowdrift game by pulling in a majority of trials to secure a share of the rewards. They acted strategically, increasing their latency to pull across the study period.
Study 4b	Children took turns to solve a Prisoner's Dilemma game. They waited longer to pull in Prisoner's Dilemma trials but, overall, decreased their latencies across the study period

### *Discussion of the findings*

When 5-year old children were presented with conflict situations in the form of Snowdrift and Prisoner's Dilemma games, I found that in line with previous research (Grueneisen et al., 2016; Melis et al., 2016), children coordinated their decisions to deal with the conflict situations presented. However, children substantially differed in their strategies to solve each game, in their latencies to act and in the ways they communicated during each type of interaction. I would argue that these behavioural differences are the result of two key differences between the two studies reported in this dissertation.

The first difference resides in the nature of both games. Despite the fact that children faced a conflict of interest to be resolved in both tasks, in the Snowdrift game unilateral cooperation was always rewarded whereas in the Prisoner's Dilemma it resulted in the worse possible outcome (Sugden, 1986; Rapoport & Chammah, 1965). The second difference refers to the way the conflicts were presented. In both studies we contrasted the *game* condition (either the Snowdrift or the Prisoner's Dilemma condition) with a *competitive* condition in which it was always better for a child to be faster than his or her partner to retrieve the highest amount of rewards; in *competitive* trials there was no need to

wait. In the Snowdrift study, both conditions were randomly presented within sessions (Study 2b in Chapter 2). In contrast, in the Prisoner's Dilemma study, each condition was presented separately (Study 4b in Chapter 3).

Given these differences, children adopted specific strategies to solve each type of conflict. In the Snowdrift game children developed a strategy that consisted of pulling on every trial to obtain rewards, the "both-partners-pull" strategy. This strategy might have been the result of children experiencing that they could always secure a share of the rewards on every trial. In fact, direct pulls resulted in rewards for both pair members on most trials. Therefore, it is not surprising that children used this strategy to solve the task while they increased the competitive nature of the game. Moreover, a complex strategy such as turn-taking would have been cognitively demanding for 5-year old children in this task. Besides the cognitive requirements necessary for effective turn-taking (see Stevens & Hauser, 2004), 5-year old children would have needed to keep track of all previous outcomes (both in Snowdrift and *competitive* trials) to maximize efficiency. In contrast, in the Prisoner's Dilemma, unilateral pulls only guaranteed the acquisition of rewards in *competitive* trials. This contingency, made evident through the training, likely allowed children to better understand the risk involved in the task. In support of this hypothesis, children established a turn-taking strategy to coordinate their actions in both the Prisoner's Dilemma and the *competitive* trials and thus, secure a fair proportion of the rewards for each child. Moreover, the repeated presentation of the same condition within sessions presumably helped children to establish and maintain the turn-taking strategy. In contrast to the "both-partners-pull" strategy, the turn-taking strategy reduced the competitive nature of the game despite the conflict of interest presented.

Thus, by focusing on the strategies children developed to overcome both types of conflicts, we could wrongly conclude that they only behave strategically in the Prisoner's Dilemma task. However, this picture clearly changes when we focus on their latencies to act.

In both tasks children waited longer to pull during the *game* conditions. In other words, when their interests conflicted, each preferred the other to pull. At the same time, they were faster in *competitive* trials to obtain the highest reward before their partner. Thus, from the results of their latencies I inferred that they distinguished both conditions and acted strategically to maximize their rewards. Yet, there were clear differences between the two studies in the way children waited. In the Snowdrift study, children became more strategic across the study period, waiting longer to pull across Snowdrift trials but, at the same time, reducing their latencies in *competitive* ones. In line with this strategy, their latencies clearly reflected the way children competed to obtain the rewards: they tried to maximize their rewards by waiting up to a certain point. Then, they preferred to pull and secure the

rewards. In that sense, children were acting rationally according to the payoffs of the game, preferring to cooperate when their partners defect to avoid the worst outcome (mutual defection). In contrast, children became faster across the Prisoner's Dilemma study in both conditions, waiting slightly more to pull in Prisoner's Dilemma trials. The fact that children became faster might be strongly related to the strategy they used to coordinate in this task; once the turn-taking sequence was established between the pair members (through the formation of a joint goal), children did not need to wait for each other to act.

Finally, I found that children communicated differently between the studies presented in this dissertation. During the Snowdrift study, children competed more to obtain the highest share of the rewards and this was reflected in the way in which they communicated. They mainly used communicative acts to coordinate in Snowdrift trials. This makes sense if we consider that children preferred their partners to pull in that condition (evident from their increased latencies to pull across time). Moreover, in the Snowdrift trials they mainly used *imperatives* to influence their partners' decisions for their own benefit. In contrast, in the Prisoner's Dilemma task, children used a turn-taking strategy to divide their rewards. Therefore, although children tended to wait longer during Prisoner's Dilemma trials, I would argue that they treated both conditions similarly. In line with this argument, children did not differ in their use of communication between conditions. Moreover, in contrast to the Snowdrift study, they did not only use *imperatives* to guide their partner's actions but also *informatives* to inform their partners about their decisions and actions. These forms of communication likely helped children to maintain efficient coordination through the study period.

### *Findings in the context of human cooperation*

The findings presented in this dissertation add to previous results by exploring children's strategies to coordinate in different scenarios of conflict (Grueneisen et al., 2016; Melis et al., 2016). A general finding of the studies presented is that by the age of 5-year old, children are able to coordinate their actions and adjust their strategies and communication according to different types of conflict presented.

The results of this dissertation are consistent with findings showing that, between the ages of three to five, children are already able to coordinate their actions to achieve common goals (Wyman et al., 2013) and they use communication to coordinate their decisions effectively (Duguid et al., 2014). At this stage of development, children also begin to see their cooperative partners as potential

reciprocators and to care about their own reputation as good cooperators (Engelmann, Herrmann & Tomasello, 2012; Sebastián-Enesco & Warneken, 2015; Warneken & Tomasello, 2013). Moreover, the results of this work are also consistent with finding showing that, between three to five years of age, children begin to understand the normative side of cooperation, feeling mutually committed to collaborate through the formation of joint goals and feeling obligated to keep up with their promises (Hamann et al., 2011; Kanngiesser, Köymen & Tomasello, 2017; Tuomela, 2006; Warneken et al., 2012; see Melis & Warneken, 2016 for a comparative review). The formation of joint goals with partners is therefore likely to be key in the establishment of efficient cooperative strategies based on “strategic trust” (Tomasello, 2016) such as turn-taking.

Overall, the development of these cognitive abilities through ontogeny are necessary for the development of later human strategic abilities to cooperate in situations of competing interests (Blake et al., 2015; Kümmerli et al., 2007; see also Sally & Hill, 2006 for a positive relationship between Theory of Mind abilities and strategic behaviour in later childhood).

### *Insights into the evolution of human cooperation*

The findings of this dissertation are in line with the Interdependence Hypothesis (Tomasello, 2012), which states that at some point in our evolutionary history, humans began to depend even more (in comparison to other social species) on their collaborative partners to survive. Thus, they were selected for their abilities to coordinate in collaborative endeavours, paving the way for the evolution of contemporary humans. Over the course of evolution, early human coordinative abilities for collaborative foraging likely had a spillover effect into more drastic situations such as when individuals needed to coordinate their actions in the face of adversity (e.g., defence against other predators). These types of situations would have further contributed to the selection of cooperative and trustworthy individuals, capable of coordinating even when this conflicts with their personal interest. This predicts a distinction between apes and human cognitive abilities to coordinate with others. In fact, this is what we see in the studies presented in this dissertation. Chimpanzees and bonobos used simpler, though specific, strategies to coordinate and maximize their rewards, in line with field observations in contexts of conflict (Gilby et al., 2015). In contrast, children used more elaborate strategies to coordinate their actions over time and to secure equal shares between pair members, especially in those cases in which the conflict was very evident.

### *5.3 Conclusion*

By adapting the Snowdrift and the Prisoner's Dilemma models, we have advanced our understanding of chimpanzees, bonobos and children's capacities to coordinate in situations of conflict of interest. The results of my studies have demonstrated that the three species were successful at solving different situations of conflict, showing some similarities in the ways they coordinated their actions, especially when those conflicts were difficult to predict and their own actions resulted in direct benefits. At the same time, the findings support the idea that children possess uniquely cognitive abilities to coordinate, allowing them to develop more efficient strategies to overcome situations of conflict.





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## APPENDICES

### *Ethical note*

The ape' studies presented in the thesis (Studies 1, 2a, 3 and 4a) were 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.

All children that participated in Studies 2b and 4b were recruited from a database of children whose parents had provided written consent to take part in child development and comparative studies, and in accordance with all applicable laws and rules governing psychological research in Germany.

### *General analysis for all studies*

All the analyses included in this thesis (except binomial tests in Studies 2a, 2b, 4a and 4b) 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). 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 when required.

All full models were compared to a null model excluding all the test variables. Only when the comparison between the full and the null model was significant we further investigate the significance of the test variables. In some occasions, we reduced models that were almost significant after discussing the procedure with a statistician). The drop1 function of the lme4 package (Bates, 2010) was used to test each variable's significance (including possible interactions between test predictors). Non-significant interactions were removed to produce a new reduced model. A likelihood ratio test with significant set at  $p < 0.05$  was used to compare models and to test the significance of the individual fixed effects (Barr, Levy, Scheepers & Tily, 2013). The 95% confidence intervals (CI) of the reduced models were calculated when appropriate.

Moreover, to rule out collinearity, Variance Inflation Factors (VIF) were checked (Field, 2005). All VIF values were closer to 1. For every model, model stability was assessed 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. 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). These general effect sizes were not considered informative for the purpose of these studies and were not reported.

## Chapter 1 Study 1

### Subjects' information Study 1

Table A1: Subjects' information for Study 1 in Chapter 1.

Name	Sex	Age (years)	Paired with (phase 1)	Paired with (phase 2)
Corrie	F	38	Fraukje	Ulla
Fraukje	F	38	Corrie	Kara
Frodo	M	21	Lome	Riet
Kara	F	9	Lobo	Sandra
Kofi	M	9	Ulla	Lobo
Lobo	M	10	Kara	Kofi
Lome	M	13	Frodo	Robert
Riet	F	37	Robert	Frodo
Robert	M	39	Riet	Lome
Sandra	F	21	Tai	NA
Tai	F	12	Sandra	NA
Ulla	F	34	Kofi	Corrie



### *Model Information Study 1*

When the data for this study was analysed, 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.

#### **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 where both subjects waited before the security peg was released ( $N = 586$ ). 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. Phase was included 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 comparison between the full and the null model was significant (GLMM:  $\chi^2_8 = 17.004$ ,  $N = 586$   $p = 0.03$ ). Two non-significant interactions were dropped from the model: the interaction between weight condition and type of trial (LMM:  $\chi^2_1 = 0.066$ ,  $N = 586$ ,  $p = 0.797$ ) and the interaction between weight condition and session number (LMM:  $\chi^2_1 = 0.556$ ,  $N = 586$ ,  $p = 0.456$ ). A significant interaction between weight condition and trial was found indicating that subjects waited longer to pull at the end of high weight sessions (see Table A2).

Table A2: 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	<b>0.013</b>	-0.195/-0.022

### 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; the control variables were sex of the individuals as fixed effect; subject, partner and dyad as random effects and the random slopes. The comparison between the full and the null model was not significant (GLMM:  $\chi^2_2 = 1.265$ ,  $N = 166$ ,  $p = 0.26$ ) suggesting that subjects did not differ between weight conditions when they were alone.

### Model 3. Time spent pulling by at least one subject (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 where 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. The comparison between the full and the null model was significant (LMM:  $\chi^2_8 = 32.73$ ,  $N = 586$ ,  $p < 0.0001$ ). Two non-significant interactions from the model were dropped: the interaction between weight condition and type of trial (LMM:  $\chi^2_1 = 2.177$ ,  $N = 586$ ,  $p = 0.14$ ) and the interaction between weight condition and session number (LMM:  $\chi^2_1 = 0.013$ ,  $N = 586$ ,  $p = 0.909$ ). A significant interaction between weight condition and trial was found suggesting that subjects got slightly faster across high weight sessions (See Table A3).

Table A3: 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	<b>0.001</b>	0.047/0.188

#### Model 4. Likelihood to cooperate (GLMM)

Model 4 investigated each dyad's likelihood to pull together. In this model we included all the data ( $N = 702$ ). We transformed the "measure of equality" (ME) into a binomial response where 1 meant both pulling and 0 meant that only one subject pulled. Cooperation was expected 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. Phase was included 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. The comparison between the full and the null model was marginally significant (GLMM:  $\chi^2_8 = 13.457$ ,  $N = 702$ ,  $p = 0.097$ ). Therefore, due to the observed trend ( $p < 0.1$ ). We inspected how the test variables contributed to the response. Two non-significant interactions were dropped from the model: the interaction between weight condition and type of trial (GLMM:  $\chi^2_1 = 0.314$ ,  $N = 702$ ,  $p = 0.575$ ) and the interaction between weight condition and trial number (GLMM:  $\chi^2_1 = 0.106$ ,  $N = 702$ ,  $p = 0.745$ ). We found an almost significant interaction between weight condition and session number suggesting that subjects pulled together more often during the last high weight sessions (see Table A4).

Table A4: 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
Sex of dyad	-	-	9.919	2	0.007	-
Total time until they touch the reward	0.562	0.258	3.497	1	0.061	0.114/1.199
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	<b>0.06</b>	-1.911/-0.108

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

Model 5 investigated the dyad's degree of cooperation. The response of the model was the ME. This model only took into account the dyads that pulled together ( $N = 490$ ). We expected subjects to cooperate more in high weight condition (especially in short time trials where the risk of losing the reward were higher). At the same time, cooperation was expected to increase across sessions and/or trials in high weight trials as a consequence of the experience pulling together. In contrast, in low weight trials subjects were not expected 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 comparison between the full and the null model was not significant (LMM:  $\chi^2_8 = 9.716$ ,  $N = 490$ ,  $p = 0.286$ ) indicating that the test variables did not significantly contribute to the subjects degree of cooperation.

### **Model 6. Difference in weight between 1<sup>st</sup> and 2<sup>nd</sup> 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. The comparison between the full and the null model was significant (LMM:  $\chi^2_4 = 10.268$ ,  $N = 478$ ,  $p = 0.031$ ). Two non-significant interactions were dropped from the model: the interaction between weight condition and type of trial (LMM:  $\chi^2_1 = 1.074$ ,  $N = 478$ ,  $p = 0.3$ ) and the interaction between weight condition and trial number (LMM:  $\chi^2_1 = 0.0009$ ,  $N = 478$ ,  $p = 0.976$ ). A significant interaction between weight condition and session was found significant suggesting that the 1<sup>st</sup> puller pulled more weight in later sessions of the high weight (see Table A5).

Table A5: 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	<b>0.007</b>	-0.103/-0.021

### 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 1<sup>st</sup> puller compared to the 2<sup>nd</sup> 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.

### 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:  $\chi^2_1 = 0.268$ ,  $N = 20$ ,  $p$

= 0.605). 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, a bootstrapping (`boot.glm` function in R) was used to calculate the confidence intervals (CI). Subject's rates of pulled weight differed significantly from 0 (no difference in subject's response in relation to weight between different partners) ( $X = 45.89$ , CI [27.84, 63.56]) 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 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 where subjects had previous experience with a partner. As a response we used the ME. 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. The comparison between the full and the null model was non-significant (GLMM:  $\chi^2_8 = 6.202$ ,  $N = 1228$ ,  $p = 0.4$ ).

*Chapter 2 Studies 2a and 2b*

*Subjects' information Study 2a*

*Table A6: Subject information for Study 2a in Chapter 2.*

<b>Name</b>	<b>Species</b>	<b>Sex</b>	<b>Age (years)</b>	<b>Paired with (phase 1)</b>	<b>Paired with (phase 2)</b>
Fimi	Bonobo	F	7	Yasa	Kuno
Gemena	Bonobo	F	10	Luisa	Yasa
Kuno	Bonobo	M	19	Lexi	Fimi
Lexi	Bonobo	F	16	Kuno	Luisa
Luiza	Bonobo	F	10	Gemena	Lexi
Yasa	Bonobo	F	18	Fimi	Gemena
Frodo	Chimpanzee	M	21	Lome	Riet
Kara	Chimpanzee	F	9	Lobo	Sandra
Kofi	Chimpanzee	M	9	Natascha	Lobo
Lobo	Chimpanzee	M	10	Kara	Kofi
Lome	Chimpanzee	M	13	Frodo	Robert
Natascha	Chimpanzee	F	34	Kofi	Tai
Riet	Chimpanzee	F	37	Robert	Frodo
Robert	Chimpanzee	M	39	Riet	Lome
Sandra	Chimpanzee	F	21	Tai	Kara
Tai	Chimpanzee	F	12	Sandra	Natascha



*Model information Study 2a***Model 9. Waiting time before pulling (LMM)**

Model 9 investigated how long the first individual waited to pull. In this model we included the trials where at least one subject pulled one rope ( $N = 1019$ ). The response was the time (in seconds) that a subject waited before start pulling. We expected subjects to maximize their rewards by waiting longer to pull in Snowdrift condition and pull faster in the *competitive* condition. We also expected them to wait longer to pull in Snowdrift condition across trials and or sessions. We included phase as a test predictor to see 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 condition, session, trial, phase and species as well as the interactions between condition and session and between condition and trial. The control variables were sex of the dyad as fixed effect; subject on the right, subject on the left and dyad as random effects and the random slopes. The comparison between the full and the null model was significant (LMM:  $\chi^2_7 = 16.588$ ,  $N = 1019$ ,  $p = 0.02$ ). We dropped the two non-significant two-way interactions between condition and session (LMM,  $\chi^2_1 = 1.135$ ,  $N = 1019$ ,  $p = 0.29$ ) and between condition and trial (LMM:  $\chi^2_1 = 1.452$ ,  $N = 1019$ ,  $p = 0.23$ ). We found a main effect of condition and trial (see Table A7). Apes pulled faster in *competitive* trials and reduced their latency to pull in both conditions within sessions.

Table A7: Model 9.

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	0.355	0.125	-	-	-	0.029/0.697
Phase	0.01	0.07	0.02	1	0.886	-0.184/0.212
Sex of dyad	-	-	4.37	2	0.112	-
Session	0.02	0.028	0.477	1	0.489	-0.59/0.0987
Trial	-0.039	0.016	4.866	1	<b>0.027</b>	-0.082/0.007
Species	0.037	0.158	0.055	1	0.815	-0.386/0.488
Condition	0.266	0.077	9.181	1	<b>0.002</b>	0.057/0.483

Table A8. Percentage of times in which each subject obtained 4 rewards.

Subject	Species	Sex	% of trials in which a subject obtains 4 rewards
Lobo	Chimpanzee	Male	65
Gemena	Bonobo	Female	59
Lome	Chimpanzee	Male	54
Riet	Chimpanzee	Female	54
Kara	Chimpanzee	Female	52
Lexi	Bonobo	Female	52
Sandra	Chimpanzee	Female	52
Fimi	Bonobo	Female	50
Natasha	Chimpanzee	Female	49
Kuno	Chimpanzee	Male	49
Frodo	Chimpanzee	Male	48
Tai	Chimpanzee	Female	46
Luisa	Bonobo	Female	45
Robert	Chimpanzee	Male	42
Yasa	Bonobo	Female	40
Kofi	Chimpanzee	Male	34

**Model 10. Distribution of conflict trials (GLMM)**

Model 10 investigated the predictors of conflict trial occurrences (trials in which both subjects pulled). In this model we included all trials except the first trials of each session ( $N = 895$ ). We transformed our response into a binomial response where 1 meant that both subjects pulled and 0 meant that only one subject pulled. We expected that previous conflict trials would decrease the likelihood of a subsequent conflict trial. We also expected more conflict trials in the *competitive* condition compared to the Snowdrift condition. Finally, we also expected that conflict trials would decrease across trials, session and phase. The full model included the test variables condition, trial, session, phase, previous conflict trial and species. The control variables were sex of the dyad as fixed effect; subject on the right, subject on the left and dyad as random effects and the random slopes. The comparison between the full and the null model was marginally significant (GLMM:  $\chi^2_6 = 11.49, N = 895, p = 0.074$ ). Therefore, due to the observed trend, we inspected how the test variables contributed to the response although we did not calculate the confidence intervals for the estimates. We found that

condition was significant suggesting that there were more conflict trials in the *competitive* condition (see Table A9).

Table A9: Model 10.

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value
Intercept	-1.437	0.704	-	-	-
Phase	-0.187	0.385	-0.062	1	1
Sex of dyad	-	-	5.286	2	0.071
Session	-0.429	0.341	1.452	1	0.228
Trial	-0.131	0.166	0.461	1	0.497
Species	0.553	0.88	0.126	1	0.723
Condition	-2.186	0.857	6.607	1	<b>0.01</b>
Prev. Conf. Trial	-0.654	0.409	1.636	1	0.2

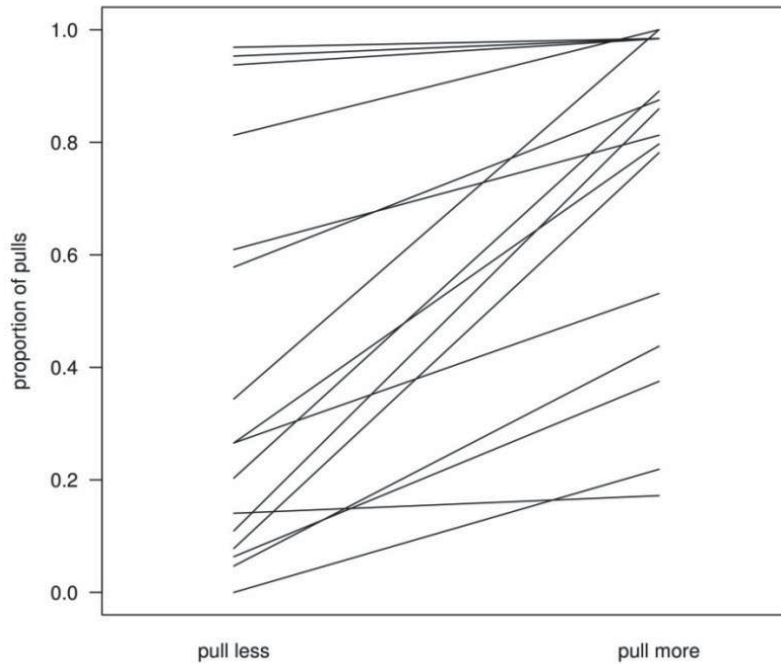


Figure A1. Graph showing the proportion of trials pulled when paired with each of the two partners. Each line end represents the proportion of pulls by a subject when paired with the partner with whom the subject pulled less (left side) and with whom the subject pulled more (right side), if pulling rate had been equal across partners we would have expected to see flat lines for each subject.

### Model information Study 2b

#### Model 11. Waiting time before pulling (LMM)

Model 11 investigated how long the first child waited to pull. We only included the trials in which at least one subject pulled the rope ( $N = 478$ ). The response was the time (in seconds) that a subject waited before starting to pull after the onset of the trial. We also expected that they would wait longer to pull in Snowdrift condition across trials and sessions. The full model included the test variables condition, session, trial as well as the interactions between condition and session and between condition and trial. The control variables were sex of the dyad as fixed effect; subject on the right, subject on the left and dyad as random effects and the random slopes. The comparison between the full and the null model was significant (LMM:  $\chi^2_5 = 18.117$ ,  $N = 478$   $p = 0.002$ ). We dropped the non-significant two-way interaction between condition and trial (LMM,  $\chi^2_1 = 0.019$ ,  $N = 478$ ,  $p = 0.89$ ). We found a significant two-way interaction between condition and session suggesting that children got slightly slower across sessions in the Snowdrift condition and slightly faster in the *competitive* conditional. We also found a significant main effect of trial (see Table A10).

Table A10: Model 11.

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	0.347	0.052	-	-	-	0.214/0.498
Sex of dyad	-	-	0.523	1	0.469	-0.27/0.152
Trial	-0.037	0.018	3.905	1	0.048	-0.083/0.011
Condition *session	0.105	0.046	4.913	1	<b>0.027</b>	-0.023/0.223

### Model 12. Distribution of conflict trials (GLMM)

Model 12 investigated what predicted the appearance of a conflict trial. In this model we included all trials except the first trial of each session ( $N = 420$ ). We transformed our response into a binomial response where 1 meant that both children pulled and 0 meant that only one child pulled. We expected that previous conflict trials would decrease the likelihood of a subsequent conflict trial. We also expected more conflict trials in the *competitive* condition compared to the Snowdrift condition. Finally, we also expected that conflict trials could decrease across trials and sessions. The full model included the test variables condition, trial, session and previous conflict trial. The control variables were sex of the dyad as fixed effect; subject on the right, subject on the left and dyad as random effects and the random slopes. The comparison between the full and the null model was non-significant (GLMM:  $\chi^2_4 = 5.305$ ,  $N = 420$ ,  $p = 0.257$ ).

### Model 13. Communication (GLMM)

Model 13 investigated the occurrence of communication. In this model we included all trials ( $N = 480$ ). We transformed our response into a binomial response where 1 meant the presence of any communicative act within the members of the dyad in a given trial and 0 meant no presence of communicative acts within the members of the dyad in a given trial. We expected children to communicate more in the Snowdrift condition. We also expected children to communicate more across trials or sessions. The full model included the test variables condition, trial and session. The control variables were sex of the dyad as fixed effect; subject on the right, subject on the left and dyad as random effects and the random slopes. The comparison between the full and the null model was

significant (GLMM:  $\chi^2_3 = 8.165$ ,  $N = 480$ ,  $p = 0.043$ ). We found a significant effect of condition suggesting that children communicated more during Snowdrift trials (see Table A11).

Table A11: Model 13.

Test category (reference category)	Estimate	Standard Error	Chi- square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	-2.276	0.769	-	-	-	-5.617/-0.138
Sex of dyad	-1.805	1.186	2.232	1	0.135	-5.741/1.506
Trial	0.079	0.150	0.253	1	0.615	-0.359/0.557
Session	0.447	0.228	3.093	1	0.079	-0.274/1.21
Condition	1.087	0.444	4.719	1	<b>0.03</b>	-0.219/2.464

## Chapter 2 Study 3

### Subjects' information Study 3

Table A12: Subjects' information for Study 3 in chapter 2.

Name	Species	Sex	Age (years)	Paired with (phase 1)	Paired with (phase 2)	Paired with (phase 3)
Fimi	Bonobo	F	8	Yasa	Gemena	Kuno
Gemena	Bonobo	F	11	Kuno	Fimi	Yasa
Kuno	Bonobo	F	20	Gemena	Yasa	Fimi
Yasa	Bonobo	F	19	Fimi	Kuno	Gemena
Bangolo	Chimpanzee	M	6	Frodo	Sandra	Lobo
Frodo	Chimpanzee	F	22	Bangolo	Taï	Sandra
Kara	Chimpanzee	M	10	Lome	Lobo	Kofi
Kofi	Chimpanzee	F	10	Lobo	Lome	Kara
Lobo	Chimpanzee	M	11	Kofi	Kara	Bangolo
Lome	Chimpanzee	M	14	Kara	Kofi	Taï
Sandra	Chimpanzee	F	22	Taï	Bangolo	Frodo
Taï	Chimpanzee	F	13	Sandra	Frodo	Lome

*Model information Study 3*

**Model 14. Choices (GLMM)**

Model 14 investigated whether apes adjusted their choices according to the number of food rewards in the social and the non-social options. In this model we included all trials in which a subject accessed either the social or the non-social option and we removed the trials where they did not access any option (in total:  $N = 2218$ ). We transformed our response into a binomial response where 1 meant that the subject chose the social option and 0 meant that the subject chose the non-social option. We expected apes to choose the social option more often when there was food only present in the tray and the non-social option, more often that when there were five items present in the alternative platform. We also expected that they will switch from the social to the non-social option more abruptly in the Snowdrift condition compared to the *competitive* condition. We also investigated whether species differed in their choices. The full model included the test variables social condition, level of non-social condition and species as well as the three-way interaction between social condition, non-social condition and species. The control variables were sex of the dyad, session, trial and phase as fixed effects; subject, partner, dyad and trial id (to account for non-independence of data points) as random effects and the random slopes. The comparison between the full and the null model was significant (GLMM:  $\chi^2_7 = 74.184$ ,  $N = 2218$ ,  $p < 0.001$ ). We dropped the non-significant three-way interaction between social condition, non-social condition and species (GLMM:  $\chi^2_1 = 1.029$ ,  $N = 2218$ ,  $p = 0.31$ ). We found a significant two-way interaction between social condition and non-social condition (see Table A13).



Table A13: Model 14.

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	0.238	0.847	-	-	-	-2.165/2.828
Phase	-0.367	0.191	3.347	1	0.067	-0.914/0.188
Sex of dyad	-	-	2.143	2	0.342	-
Trial	0.181	0.078	5.418	1	0.019	-0.046/0.409
Session	-0.202	0.107	3.256	1	0.071	-0.519/0.103
Species	-0.971	1.031	0.85	1	0.356	-3.814/2.086
Social condition*non-social condition	1.213	0.346	9.572	1	<b>0.002</b>	0.284/2.258

### Model 15. Latencies to open the door (LMM)

Model 15 investigated the length of time from the start of the trial (when the experimenters released the security pegs) until the moment the subjects open the door to access either the social or the non-social option. In this model we included the trials in which an opening action occurred ( $N = 2216$ ). The response was the time (in seconds) that a subject took to open one of the doors. We expected subjects to open the door faster in *competitive* trials compared to Snowdrift trials and we also expected a decrease in their latencies in relation to an increase in the number of items presented in the non-social option. We expected the decrease in latency to follow a quadratic distribution. In other words, we hypothesized the decrease in latency to be unequal between conditions, being larger between 0 and 1 levels of the non-social option during Snowdrift trials. For this reason we included a squared term for the non-social option. We also investigated whether chimpanzees and bonobos would differ in their latencies to open the door. The full model included the test variables social condition, level of non-social condition and species as well as the three-way interaction between social condition, non-social condition, and species. The control variables were sex of the dyad, session, trial, phase and choices as fixed effects; subject, partner, dyad and trial id as random effects and the random slopes. The comparison between the full and the null model was significant (GLMM:  $\chi^2_{12} = 52.856$ ,  $N = 2216$ ,  $p < 0.001$ ). We dropped the non-significant three-way interaction between social condition, non-social condition and species (GLMM:  $\chi^2_1 = 1.31$ ,  $N = 2216$ ,  $p = 0.31$ ). We found a significant two-way

interaction between social condition and non-social condition and also a main effect of species; overall, chimpanzees opened the door faster than bonobos (see Table A14 and Figure A2).

Table A14: Model 15.

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	0.368	0.137	-	-	-	-0.004/0.717
Phase	-0.094	0.037	4.884	1	0.027	-0.203/0.008
Sex of dyad	-	-	6.711	2	0.0348	-
Trial	-0.027	0.035	0.6	1	0.438	-0.12/0.069
Session	-0.032	0.043	0.546	1	0.459	-0.144/0.09
Choice	-0.637	0.134	14.47	1	0.0001	-1.029/-0.264
Species	-0.567	0.171	8.06	1	<b>0.004</b>	-1.061/-0.099
Squared non-social condition	0.148	0.034	11.697	1	0.0006	-0.053/0.243
Social condition*non-social condition	0.156	0.051	6.62	1	<b>0.01</b>	-0.007/0.295

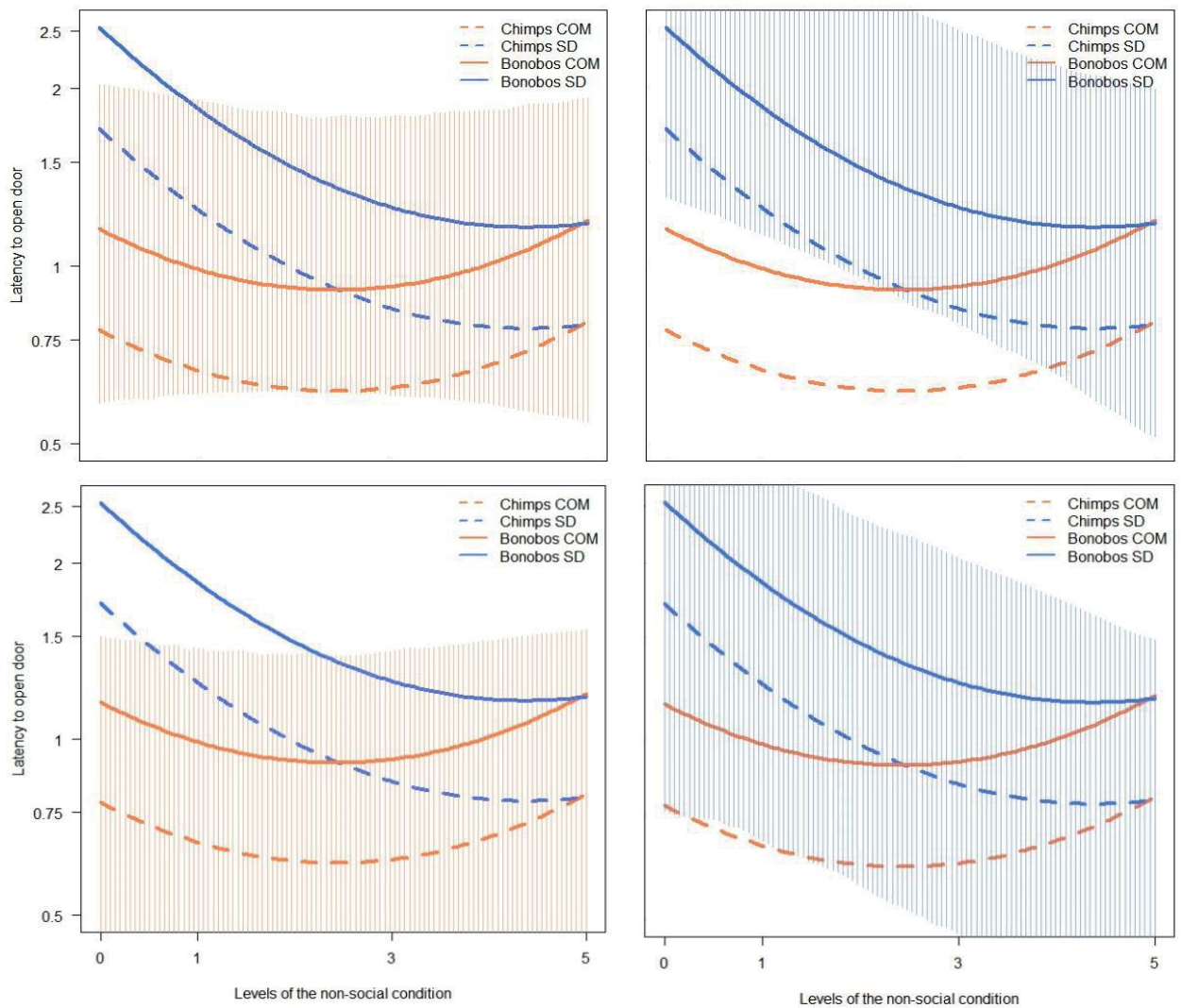


Figure A2. Latency of the subjects to open the door as a function of the number of food pieces in the non-social option and the social option (Snowdrift (SD) and competitive (COM) trials). Each figure depicts a CI. Top left Bonobos COM, top right Bonobos SD, bottom left Chimpanzees COM, bottom right Chimpanzees SD. Latencies in seconds are presented in a logarithmic scale.

### Model 16. Latencies to pull the ropes (LMM)

Model 16 investigated the length of time from the moment a subject opens the door to the social option only until they start pulling on the rope. In this model we included the trials in which pulling occurred ( $N = 773$ ). The response was the time (in seconds) that a subject took to pull the rope. We expected subjects to pull faster in *competitive* trials compared to Snowdrift trials. We investigated whether the presence of food in the non-social option (although not available anymore for the

subject) had an effect on the latency to pull the rope. We also tested whether chimpanzees and bonobos would differ in their latencies to pull. The full model included the test variables social condition, level of non-social condition and species as well as the three-way interaction between social condition, non-social condition and species. The control variables were sex of the dyad, session, trial and phase as fixed effects; subject, partner, dyad and trial id as random effects and the random slopes. The comparison between the full and the null model was significant (LMM:  $\chi^2_8 = 31.236$ ,  $N = 773$ ,  $p < 0.001$ ). We found a significant three-way interaction between social condition, non-social condition and species (see Table A15 and Figure A3). In this model we had to make a correction *a posteriori*. We removed three outliers we did not detect in an earlier analysis. The three way interaction and the full-null model comparison remained significant after the correction.

Table A15: Model 16.

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	0.848	0.067	-	-	-	0.663/1.044
Phase	-0.025	0.042	0.342	1	0.558	-0.145/0.084
Sex of dyad	-	-	0.896	2	0.638	-
Trial	-0.048	0.024	3.448	1	0.063	-0.116/0.014
Session	0.055	0.046	1.363	1	0.243	-0.069/0.181
Social condition*non-social condition*species	0.152	-	3.888	1	<b>0.048</b>	-0.044/0.37

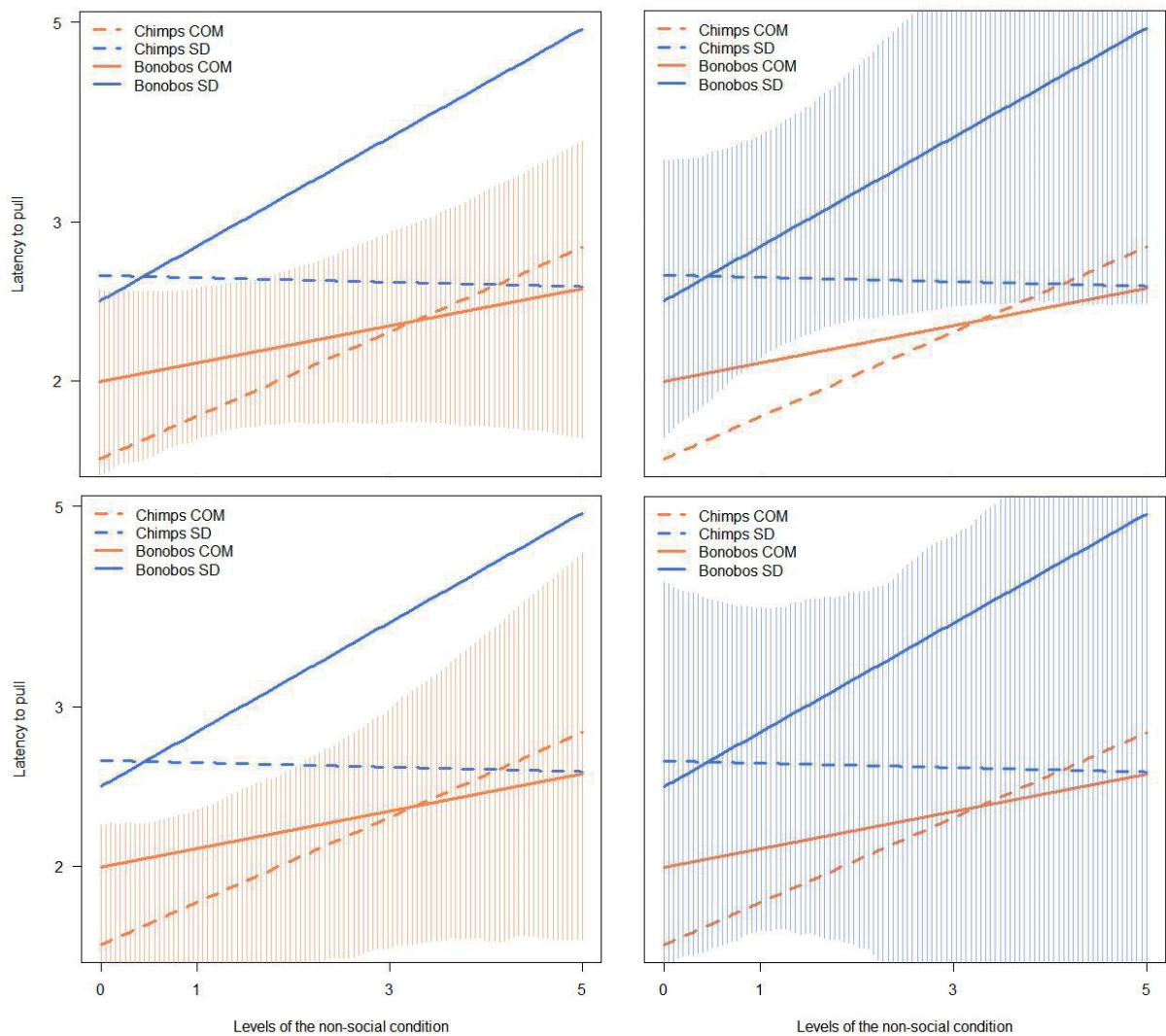


Figure A3. Latency of the subjects to pull the rope as a function of the levels in the non-social option and the social option (Snowdrift and competitive trials). Each figure depicts a CI. Top left Bonobos COM, top right Bonobos SD, bottom left Chimps COM, bottom right Chimps SD. Latencies in seconds are presented in a logarithmic scale.

### Model 17. Strategic choices of 2<sup>nd</sup> actors based on 1<sup>st</sup> actor actions (GLMM)

Model 17 investigated whether 2<sup>nd</sup> actors would make strategic choices based on the previous choices of the 1<sup>st</sup> actors. In this model we included the trials where both the 1<sup>st</sup> and 2<sup>nd</sup> actors opened the sliding door ( $N = 925$ ). We removed the trials in which both members opened their doors at the same time. To investigate the 2<sup>nd</sup> actors' strategic choices, we created a binomial variable establishing whether the choice of the 2<sup>nd</sup> actor was strategic or not based on the 1<sup>st</sup> actor decision for every combination of social and non-social conditions. We used this variable as the response variable in our

model. We expected that both social and non-social conditions would influence in the 2<sup>nd</sup> actors decisions. Moreover, we conducted pair-wise comparisons to analyse whether 2<sup>nd</sup> actors made strategic choices contingent upon the 1<sup>st</sup> actor’s decision for each combination of social and non-social conditions (8 levels in total). The full model included the test variables social condition and non-social condition as well as the two-way interaction between them. The control variables were the sex of the 1<sup>st</sup> actor, the sex of the 2<sup>nd</sup> actor, session, trial, phase and species as fixed effects; first actor, second actor and dyad as random effects and the random slopes. The comparison between the full and the null model was significant (GLMM:  $\chi^2_7 = 43.413$ ,  $N = 925$ ,  $p < 0.001$ ). We found a significant two-way interaction between social condition, and non-social condition (see Table A16). The pair-wise comparisons revealed that 2<sup>nd</sup> actors were making strategic choices in 4 of 8 combinations (see Figure 17 in Chapter 3).

Table A16: Model 17.

Test category (level 5 non-social, COM condition)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	2.563	0.733	-	-	-	0.531/22.301
Level 0	2.842	1.266	-	-	-	-0.811/22.118
Level 1	-0.278	0.885	-	-	-	-18.633/2.596
Level 3	-2.416	0.881	-	-	-	-20.995/-0.126
Phase	0.031	0.198	0.025	1	0.875	-0.548/0.696
Session	-0.015	0.156	0.009	1	0.926	-0.548/0.499
Trial	0.047	0.127	0.14	1	0.708	-0.0367/0.444
Species	0.332	0.484	0.446	1	0.504	-1.107/1.902
Condition (Snowdrift)	2.567	1.263	-	-	-	-1.328/21.362
Social condition*non-social condition	-	-	18.54	3	<b>&lt;0.001</b>	-

### Chapter 3 Studies 4a and 4b

#### Subjects' information Study 4a

Table A17: Subject information for Study 4a in chapter 3.

\*these subjects only participated in the first phase of the test sessions.

Name	Species	Sex	Age (years)	Paired with
Alex*	Chimpanzee	M	15	Jahaga
Alexandra*	Chimpanzee	F	17	Daza
Bangolo	Chimpanzee	M	7	Sandra
Corrie	Chimpanzee	F	40	Frodo
Daza*	Chimpanzee	F	unknown	Alexandra
Dorien	Chimpanzee	F	36	Lome
Frodo	Chimpanzee	M	23	Corrie
Jahaga*	Chimpanzee	F	23	Alex
Kofi	Chimpanzee	M	9	Lobo
Lobo	Chimpanzee	M	12	Kofi
Lome	Chimpanzee	M	15	Dorien
Robert	Chimpanzee	M	41	Tai
Sandra	Chimpanzee	F	23	Bangolo
Tai	Chimpanzee	F	13	Robert

### *Model information Study 4a*

Due to the large number of trials in which chimpanzees did not wait to pull –in other words, zeros in our data-set (18% of trials), we analysed the latency measure with two different models. In the first model we explored whether chimpanzees waited or not to pull (binomial model), and in the second model we focused on the subset of the data in which they waited to pull (Gaussian model). We could not run a statistical model to explore what influences their likelihood to pull. The model was too over fitted relative to the small number of cases where no chimpanzee pulled (only 40 cases out of 760). In addition, we could not statistically analyse the duration of coordination trials during *competitive* sessions due to the small sample size of 77 coordination trials.

### **Model 18. Binomial model of latencies in chimpanzees (GLMM)**

Model 18 investigated whether chimpanzees waited or not to pull. In this model we included the trials where at least one subject pulled one rope ( $N = 720$ ). We transformed our response into a binomial response where 1 meant that the first subject waited more than 0 seconds to pull and 0 meant that the first subject did not wait to pull. We expected subjects to wait more in the Prisoner's Dilemma compared to the *competitive* condition and that this difference would increase across trials, sessions, and phases. The full model included the test variables condition, session, trial and phase as well as the interactions between condition and session, between condition and trial, and between condition and phase. The control variables were sex of the dyad as fixed effect; subject in the right, subject in the left and dyad as random effects and the random slopes. The comparison between the full and the null model was significant (GLMM:  $\chi^2_7 = 22.14$ ,  $N = 720$ ,  $p = 0.002$ ). We dropped the two non-significant two-way interactions: the interaction between condition and trial (GLMM,  $\chi^2_1 = 3.41$ ,  $N = 720$ ,  $p = 0.064$ ) and the interaction between condition and phase (GLMM,  $\chi^2_1 = 0.09$ ,  $N = 720$ ,  $p = 0.76$ ). We found a significant two-way interaction between condition and session suggesting that chimpanzees waited more to pull across Prisoner's Dilemma trials and waited less across *competitive* trials (see Table A18).



Table A18: Model 18.

Test category (reference category)	Estimate	Standard Error	Chi- square	Degrees of freedom	p- value	CI (95%) of the reduced model
Intercept	4.62	2.26	-	-	-	-1.47/57.56
Phase	-0.15	0.57	0.78	1	0.79	-2.62/ 2.19
Sex of dyad	-	-	0.03	2	0.98	-
Trial	-0.13	0.12	1.19	1	0.27	-0.61/ 0.36
Condition*Session	-1.75	0.55	7.61	1	<b>0.005</b>	-5.35/0.68

### Model 19. Gaussian model of latencies in chimpanzees (LMM)

Model 19 investigated how long the first individual of a pair waited to pull (only in those trials in which they waited to pull more than 0 seconds) ( $N = 590$ ). The response was the time (in seconds) that a subject waited before start pulling. We expected subjects to wait longer in the Prisoner's Dilemma condition and pull faster in the *competitive* condition. We also expected them to wait longer to pull in the Prisoner's Dilemma condition across trials, sessions and phases. The full model included the test variables condition, session, trial and phase as well as the interactions between condition and session, between condition and trial and between condition and phase. The control variables were sex of the dyad as fixed effect; subject in the right, subject in the left and dyad as random effects and the random slopes. The comparison between the full and the null model was significant (LMM:  $\chi^2_7 = 50.53$ ,  $N = 590$ ,  $p < 0.001$ ). We dropped the non-significant two-way interaction between condition and phase (LMM:  $\chi^2_1 = 0.46$ ,  $N = 590$ ,  $p = 0.5$ ). We found a significant two-way interaction between condition and session (LMM,  $\chi^2_1 = 6.41$ ,  $N = 590$ ,  $p = 0.01$ ) and between condition and trial (LMM:  $\chi^2_1 = 12.32$ ,  $N = 590$ ,  $p < 0.001$ ) suggesting that chimpanzees waited longer to pull across Prisoner's Dilemma trials and sessions but were faster across *competitive* trials and sessions (see Table A19).

Table A19: Model 19.

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	0.13	0.75	-	-	-	-2.02/1.94
Phase	-0.04	0.27	0.02	1	0.9	-0.73/0.71
Sex of dyad	-	-	1.88	2	0.39	-
Condition*Trial	-0.49	0.21	12.57	1	<b>&lt;0.001</b>	-0.77/-0.24
Condition*Session	-1.04	0.09	12.33	1	<b>&lt;0.001</b>	-1.64/-0.45

**Model 20. Binomial model of coordination in chimpanzees (GLMM)**

Model 20 investigated whether chimpanzee dyads coordinated or not to pull together. In this model we included all trials ( $N = 759$ ). We transformed our response into a binomial response where 1 meant that pairs coordinated (both pulled and divided their rewards) and 0 meant that dyads did not coordinate to collaborate. We expected dyads to coordinate more in both conditions across trials, sessions and phases. The full model included the test variables condition, session, trial and phase as well as the interactions between condition and session, between condition and trial and between condition and phase. The control variables were sex of the dyad as fixed effect; subject in the right, subject in the left and dyad as random effects and the random slopes. The comparison between the full and the null model was significant (GLMM:  $\chi^2_7 = 21.09$ ,  $N = 759$ ,  $p = 0.004$ ). We dropped the two non-significant two-way interactions between condition and trial (GLMM,  $\chi^2_1 = 1.33$ ,  $N = 759$ ,  $p = 0.25$ ) and between condition and phase (GLMM:  $\chi^2_1 = 0.23$ ,  $N = 759$ ,  $p = 0.63$ ). We found a strong trend between condition and session suggesting that chimpanzees coordinated more in *competitive* trials across sessions. Moreover, we found a main effect of phase (GLMM:  $\chi^2_1 = 5.61$ ,  $N = 759$ ,  $p = 0.018$ ) suggesting that chimpanzees coordinated more often in the second phase of the study (see Table A20).

Table A20: Model 20.

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	-5.09	1.61	-	-	-	-69.45/-4.55
Phase	0.76	0.26	5.61	1	<b>0.018</b>	-0.08/1.81
Sex of dyad	-	-	3.04	2	0.22	-
Trial	0.26	0.2	1.51	1	0.22	-0.37/0.9
Condition*Session	1.4	0.73	3.58	1	<b>0.058</b>	-0.95/40.7

### Relationship between food maximization and strategic choices

We measured the relationship between the proportion of strategic choices individuals scored and the ratio of grapes per trial that individuals obtained. To calculate the proportion of strategic choices, we summed the proportion of pulls in *competitive* + the proportion of no-pulls in Prisoner's Dilemma trials and we divided it by 2 for every individual. To calculate the ratio of grapes per trial as a measure of food maximization, we calculated a ratio between the total grapes consumed in the study divided by the total number of trials each chimpanzee performed. We found a positive correlation ( $r = 0.84$ ; Figure A4) between food maximization and strategic choices. We found that two of the *pullers* obtained substantially more grapes than one *strategiser*. These two *pullers* learned to make short pulls during Prisoner's Dilemma trials, resulting in some grapes jumping into their own bucket. Moreover, one *strategiser* obtained much less grapes than the other three *strategisers*. This *strategiser* was paired with another *strategiser* who performed better.

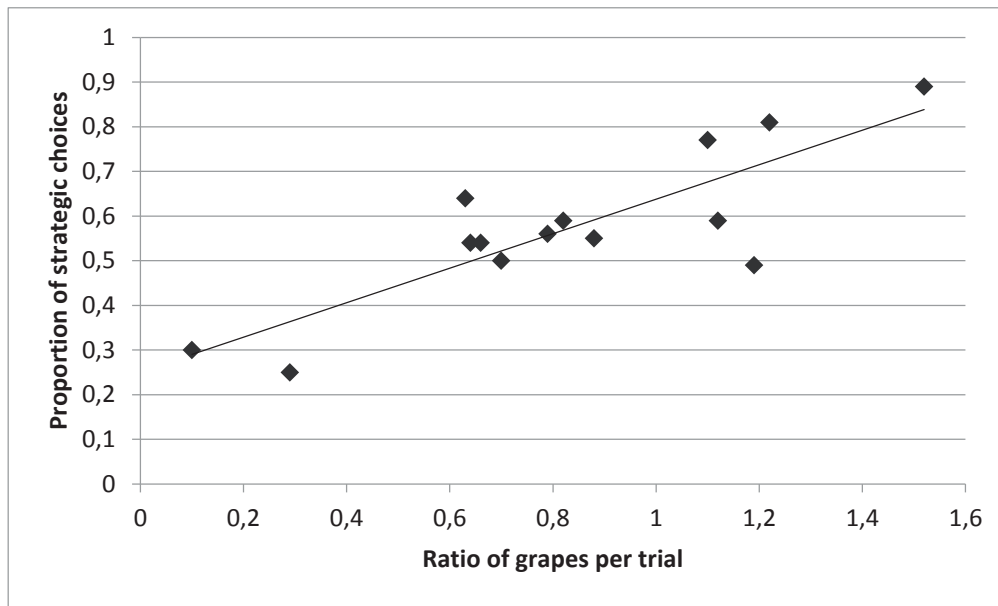


Figure A4. Positive correlation between the ratio of grapes per trial and the proportion of strategic choices. Each data point represents one subject.

Model information Study 4b

**Model 21. Gaussian model of latencies in children (LMM)**

Model 21 investigated how long the first individual of a pair waited to pull ( $N = 303$ ). The response was the time (in seconds) that a subject waited before start pulling. We removed the trials in which subjects did not pull ( $N = 15$ ) and trials in which subjects did not wait ( $N = 2$ ). We expected subjects to wait longer in the Prisoner’s Dilemma condition and pull faster in the *competitive* condition. We also expected them to wait longer to pull in the Prisoner’s Dilemma condition across trials. The full model included the test variables condition, session and trial as well as the interaction between condition and trial (children only did one session, thus we did not include the interaction between condition and session). The control variables were sex of the dyad as fixed effect; subject in the right, subject in the left and dyad as random effects and the random slopes. The comparison between the full and the null model was significant (LMM:  $\chi^2_4 = 32.56$ ,  $N = 303$ ,  $p < 0.001$ ). We dropped the non-significant two-way interaction between condition and trial (LMM,  $\chi^2_1 = 2.4$ ,  $N = 303$ ,  $p = 0.12$ ). We found a main effect of condition (LMM:  $\chi^2_1 = 6.15$ ,  $N = 303$ ,  $p = 0.013$ ) suggesting that children waited longer to pull in the Prisoner’s Dilemma condition. Moreover we found a main effect of session (LMM:  $\chi^2_1 = 7.94$ ,  $N = 303$ ,  $p = 0.005$ ) and of trial (LMM:  $\chi^2_1 = 15.59$ ,  $N = 303$ ,  $p < 0.001$ ) in the same direction suggesting that children tended to pull faster across sessions and trials. (see Table A21).

Table A21: Model 21.

Test category (reference category)	Estimate	Standard Error	Chi-square	Degrees of freedom	p-value	CI (95%) of the reduced model
Intercept	0.65	0.193	-	-	-	0.103/1.17
Sex of dyad	-	-	3.89	1	0.048	-
Session	-0.202	0.065	7.94	1	<b>0.005</b>	-0.37/-0.015
Trial	-0.282	0.056	15.59	1	<b>&lt;0.001</b>	-0.442/-0.142
Condition	0.349	0.129	6.15	1	<b>0.013</b>	0.005/0.69

### Model 22. Turn-taking model (GLMM)

Model 22 investigated whether children used a turn-taking strategy to solve the dilemma presented. In this model we excluded the first trials of every session ( $N = 40$ ) for a total of 280 trials. We transformed our response into a binomial response where 1 meant that children took a turn in a trial and 0 meant children did not take a turn. A turn was defined as the occurrence of a unilateral pull by individual A only when individual B had unilaterally pull in a previous trial. To calculate the probability that a turn-taking event occurred by chance, we assumed that children were equally likely to either defect (D) or cooperate (C) within a trial. Therefore, there were four possible outcomes within a trial (C, C; D, D; C, D and D, C). Thus, there were 16 possible combinations between two consecutive trials (the product of each trials' combination) and only two resulted in turn-taking (C, D  $\rightarrow$  D, C and D, C  $\rightarrow$  C, D). Thus, we determined that children had a probability to turn-take by chance in 12.5% of the trials (2 of 16 possible combinations). We expected children to take more turns in the Prisoner's Dilemma condition. We also expected children to develop this strategy within the Prisoner's Dilemma session. The full model included the test variables condition, session and trial as well as the interaction between condition and trial. The control variables were sex of the dyad as fixed effect; subject in the right, subject in the left and dyad as random effects and the random slopes. The comparison between the full and the null model was not significant (GLMM:  $\chi_4^2 = 2.652$ ,  $N = 280$ ,  $p = 0.634$ ). To investigate whether children took turns significantly above chance, we adjusted the averages of the model predictors such that the intercept revealed the probability of a positive response. We found that the intercept deviated from the pre-established chance level (12.5 %) (Intercept: estimate = 0.22, SE = 0.56,  $p < 0.001$ ) meaning that children significantly used a turn-taking strategy.

### **Model 23. Communication (GLMM)**

Model 23 investigated the occurrence of communication within a trial. In this model we included all trials ( $N = 320$ ). We transformed our response into a binomial response where 1 meant the presence of any communicative act between the members of the pair in a given trial (from the moment E1 showed the marbles until the last child inserted the obtained rewards in their boxes); 0 meant no presence of communicative acts in a given trial. We expected children to communicate more in the Prisoner's Dilemma condition. We also expected children to communicate more by the end of the study, as a sign of learning. The full model included the test variables condition, trial and session as well as the interaction between condition and trial. The control variables were sex of the dyad as fixed effect; subject on the right, subject on the left and dyad as random effects and the random slopes. The comparison between the full and the null model was not significant (GLMM:  $\chi^2_4 = 8.75$ ,  $N = 320$ ,  $p = 0.068$ ).

### **Relationship between rewards maximization and strategic choices**

We measured the relationship between the proportion of strategic choices that children scored and the ratio of rewards per trial that they obtained. To calculate the proportion of strategic choices and the ratio of rewards per trial, we used the methodology of Study 4a (see page 153-154). We found a moderate positive correlation between the proportion of subject's strategic choices and the amount of marbles obtained ( $r = 0.5$ ; Figure A5). Interestingly, the *strategiser* child (orange data point) did not result in the most successful subject.

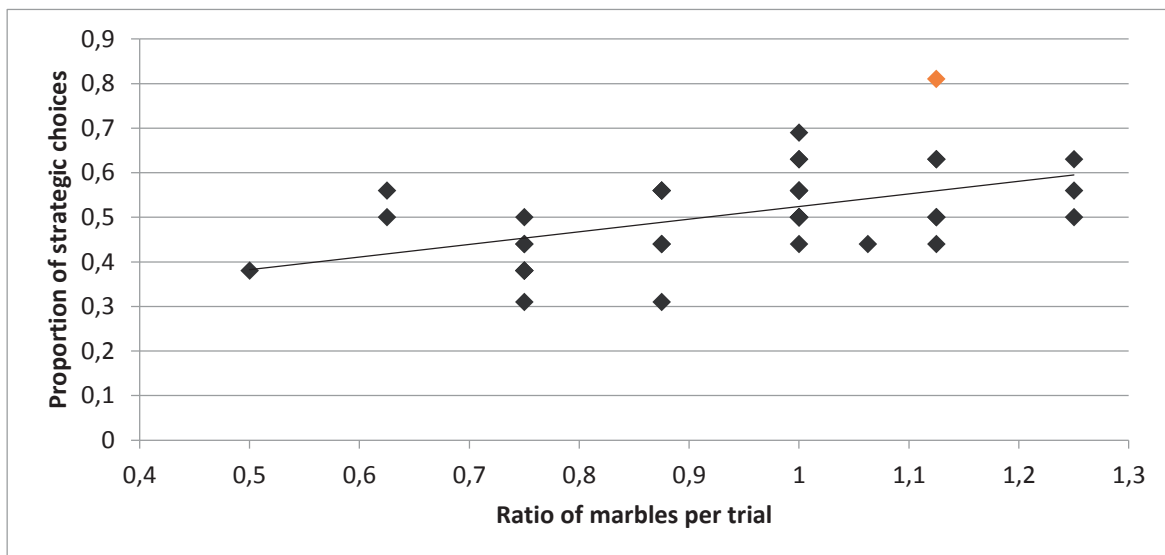


Figure A5. Positive correlation between the ratio of marbles per trial and the proportion of strategic choices. Each data point represents one subject.

## **BIBLIOGRAPHISCHE DARSTELLUNG**

**Alejandro Sánchez Amaro**

COORDINATION IN CONFLICT SITUATIONS

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*Dissertation*

182 Seiten, 267 Literaturangaben, 29 Abbildungen, 24 Tabellen

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The present dissertation investigated the strategies that great apes and 5-year old children used to coordinate in situations of conflict in an attempt to shed light on the evolution of human cooperation.

The first chapter investigated how pairs of chimpanzees coordinated their actions to overcome a conflict of interest in the form of a Snowdrift game. During the game, individuals could either cooperate or free-ride to acquire a reward. Chimpanzees successfully managed a trade-off between maintaining successful cooperation and minimizing costs.

The second chapter explored how pairs of chimpanzees, bonobos and children solved another version of the Snowdrift game. In this game, individuals could not collaborate but could take turns to reciprocate their rewards. Apes and children waited longer to act when cooperation led to the lowest reward. However, they differed in their strategies. On the one hand, children preferred to act in a majority of trials to secure a proportion of the rewards, and on the other hand apes preferred one individual to pull and thus, reduce the risk to compete for the rewards. In a follow-up, chimpanzees and bonobos were presented with the possibility to choose between the social game and a non-social alternative that provided a secure reward. In this situation, apes behaved more strategically compared to the previous task. They managed the conflict by combining information about the rewards in the social and non-social options with their partners' likely decisions.

The last chapter investigated how pairs of chimpanzees and children solved a Prisoner's Dilemma game. In this task, individuals could either cooperate alone and send all the rewards to a partner or collaborate and divide the rewards. Chimpanzees acted strategically, waiting for their partner to pull but did not reciprocate nor collaborate to obtain the rewards. In contrast, children developed a strategy based on turn-taking to reciprocate the rewards over time and thus maintain high levels of cooperation.

The findings in this dissertation suggest that all species were successful at solving different situations of conflict. While there were similarities in the ways they coordinated their actions, children showed more efficient strategies to overcome the conflict, given support to the hypothesis that over the course of evolution, humans developed uniquely cognitive abilities for cooperation.



# SUMMARY

This dissertation investigates the strategies that chimpanzees, bonobos and children use to coordinate in situations of conflict. Socially complex animals such as humans and great apes regularly need to coordinate their actions to achieve cooperative goals not attainable individually. Collaboration, acting together for mutual goals, is a solution when individuals' interests do not compete. However, in some situations, opportunities to cooperate come together with opportunities to defect. In that context, great apes and humans are likely to face conflicts of interest when they need to decide whether or not to cooperate with other group members. For instance, when chimpanzees initiate hunts in groups, some members may prefer to lag behind and wait for other chimpanzees to pay the costs related to the hunt. By presenting pairs of chimpanzees, bonobos and 5-year old children with situations of conflicting interests we can explore the strategies that these species use to coordinate their actions to overcome those conflicts in an attempt to shed light on the evolution of human cooperation.

In the first chapter of this thesis, I present pairs of chimpanzees with a conflict situation in the form of a Snowdrift game, a game theoretical model used to explore whether individuals cooperate when their interests compete (Study 1). In this game, both players can either cooperate or free-ride. Mutual cooperation results in a better reward than mutual defection. However, the key feature of this game is that it is better to defect if your partner cooperates, but better to cooperate if your partner defects; in other words, it is better to do the opposite of your partner. Returning to the example of chimpanzee hunting, 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. 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. To recreate the payoff structure of this game I presented pairs of chimpanzees with a weighted tray containing rewards for both individuals. Subjects needed to decide whether to collaborate (i.e., pull the tray together and share the costs) or pull alone and unilaterally pay the burden of cooperation. Chimpanzees had a limited amount of time to make their decisions before the rewards disappeared. The best strategy for an individual was to wait for a partner to pull and obtain the rewards when cooperative costs were high; maximizing benefits while reducing costs. Chimpanzees' performance when cooperative costs were high was compared to their performance in a low weight condition in which the costs to cooperate were minimum.

The findings showed that chimpanzees successfully coordinated their actions to overcome the conflict, obtaining the rewards the majority of times. Surprisingly, chimpanzees collaborated more often when the costs were high even though they had the opportunity to defect. However, they did not just collaborate to obtain the rewards; they showed clear signs of strategic decision-making to reduce costs. When costs were high, chimpanzees waited longer to pull, reducing the likelihood of incurring all the costs unilaterally. Moreover, when I investigated in more detail how they collaborated, I found that pairs of chimpanzees contributed unequal efforts, suggesting that they tried to minimize costs. In all, these results suggest that chimpanzees were able to manage the trade-off between successful coordination (within the time limits) and minimizing costs.

In the second chapter of the dissertation I presented pairs of bonobos and chimpanzees (Study 2a), and children (Study 2b) with a second version of the Snowdrift game. In this version of the game, in contrast to the previous one, subjects could not collaborate within trials but they could use other strategies to overcome the conflict over the course of the study (e.g., taking-turns over trials). I presented the three species with a rotatory tray baited with an unequal reward distribution. Two detachable ropes were connected to the interior end of the tray. The ropes were oriented in opposite directions and each fed into one subjects' room. Each individual could pull from their rope and move the interior end of the tray towards him while the exterior end moved towards the partner. Yet, if both individuals pulled at the same time, the ropes could detach from the tray, preventing individuals from accessing the rewards. In the Snowdrift condition, the preferred reward distribution was baited on the interior end and it could only be obtained by waiting for the partner to pull. In contrast, in a competitive condition, the reward distribution was changed (the best rewards were baited on the interior). In this second condition, the best strategy was to pull before the partner. As in the previous task, apes and children had a limited amount of time to decide on their actions. The main aim of this study was to explore whether individuals would behave strategically in this version of the game; waiting longer in the Snowdrift condition compared to the competitive one. Moreover, another aim of the study was to compare the strategies that each of the three species used to solve the conflict situation and to explore whether communication played a significant role in their performance.

The results of the study showed that the three species successfully coordinated to obtain the rewards most of times. In the critical condition, all three species waited longer to pull, showing a general understanding of the task. An analysis of their pulling strategies revealed that children learned to wait longer to pull across sessions, although they ended up pulling in most trials. In contrast, great apes were more likely to employ a strategy that consisted of only one individual pulling the majority of times in both the Snowdrift and the competitive condition. Yet, not all great apes employed this

strategy: some individuals behaved clearly strategically, pulling significantly more often during competitive than Snowdrift trials. With regard to whether apes and children used communicative acts to facilitate their coordination, I found that children but not apes communicated during the task. They used specific types of verbal communication to influence their partners' decisions for their own benefit.

Due to the strategies shown by some great apes in the first part of the study, I developed a follow-up to test chimpanzees' and bonobos' decision-making strategies in more detail (Study 3). For this purpose, I presented the same rotating tray that was used in the first part of the study (the *social* option) with the addition of an alternative secure reward for each subject (the *non-social* option). In this new context, individuals could decide whether to participate in the social dilemma or access the non-social option; inaction was no longer possible. Importantly, the quantity of the rewards presented in the non-social option varied between sessions. I hypothesized that the addition of the non-social option would allow subjects to better manage the risks and chose strategically depending on the reward distribution presented and the partners' likely decisions. Moreover, by comparing chimpanzees and bonobos, I explored species' sensitivity to social risk in a context in which those risks could be avoided by accessing the non-social option. Finally, I investigated whether individuals would take advantage of their partners' previous actions to maximize their rewards.

The results of this study showed that both great ape species coordinated to obtain the rewards in the majority of trials and behaved strategically during the task. Apes' latencies to retrieve the rewards decreased as the quantity in the non-social option increased. Moreover, once they had chosen the social option, apes still waited longer in the critical condition, when the preferred reward could only be obtained if the partner had previously acted. Both ape species increased their choices towards the non-social option as the proportion of the rewards in the non-social option increased compared to the social option. This finding suggests that there were no significant differences between chimpanzees and bonobos in their sensitivity towards social risks. Finally, I found that great apes adjusted their choices to maximize their rewards while avoiding competitive situations and anticipating partners' likely decisions.

In the last chapter of the dissertation I presented pairs of chimpanzees (Study 4a) and children (Study 4b) with a Prisoner's Dilemma situation. In contrast to the Snowdrift game, in the Prisoner's Dilemma unilateral cooperation is the worst outcome for cooperators; individuals do not benefit from their unilateral actions. To recreate the Prisoner's Dilemma I presented pairs of chimpanzees and children with a rectangular elevator baited with rewards at its ends. Each subject could pull from a rope

connected to one side of the apparatus. In the Prisoner's Dilemma condition subjects had to wait for their partners to cooperate (i.e., pull from the rope) in order to obtain the best rewards. In contrast, in a competitive condition that served as a control all the rewards could only be accessed by pulling before the partner. Moreover, in both conditions individuals could collaborate (i.e., pulling their ropes at the same time) and divide the rewards. As in previous studies, individuals had a limited amount of time to operate the apparatus and obtain the rewards.

The main aim of this comparative study was to explore whether chimpanzees and children would behave strategically in their attempts to overcome the conflict presented. I hypothesized that, because unilateral cooperation yielded no rewards for cooperators, individuals would behave more strategically in this context compared to a Snowdrift in which cooperation was always rewarded. A secondary aim of the study was to explore the strategies that individuals would use to overcome the conflict when collaboration was possible. Finally, in the case of children I was interested in the role of communication to maintain successful coordination in a Prisoner's Dilemma scenario.

The findings of this comparative work indicate that both species substantially differed in their strategies to solve the task. Chimpanzees learned to behave more strategically over the study period; in the competitive condition they pulled very quickly compared to the Prisoner's Dilemma condition in which they increased their latencies. However, chimpanzees ultimately pulled in that condition. One possible explanation for these high levels of cooperation could be that chimpanzees tried to entice their partners to pull. This transformed Prisoner's Dilemma trials into competitive trials, thereby increasing their likelihood to obtain the rewards. Children developed a more efficient strategy that consisted of taking turns to reciprocate their rewards. Interestingly, they used this strategy in both conditions. In line with this finding, they became faster across the study period; once the turn-taking strategy was established, they waited less for their partner's decisions. Finally, I found that children used specific types of communication to coordinate with their partners and maintain high levels of cooperation in both conditions, a reflection of their turn-taking strategy.

By adapting the Snowdrift and the Prisoner's Dilemma models, we have advanced our understanding of chimpanzees', bonobos' and children's capacities to coordinate in situations of conflicting interests. The results of my studies have demonstrated that the three species were successful at solving different situations of conflict, showing some similarities in the ways they coordinated their actions, especially when their own actions resulted in direct benefits. At the same time, the findings support the idea that children possess uniquely cognitive abilities to coordinate, allowing them to develop more efficient strategies to overcome situations of conflict.

# ZUSAMMENFASSUNG

In dieser Dissertation werden Strategien untersucht, mit denen sich Schimpansen, Bonobos und Kinder in Konfliktsituationen koordinieren. Sozial komplexe Tiere wie Menschen und Große Menschenaffen müssen ihr Verhalten regelmäßig untereinander koordinieren, um kooperative Ziele zu verwirklichen, die sie alleine nicht erreichen würden. Kollaboration, das heißt zusammenarbeiten für gemeinsame Ziele, stellt eine Lösung dar, wenn die Interessen der Individuen nicht im Widerspruch zueinander stehen. In manchen Situationen gehen allerdings Gelegenheiten zu kooperieren mit Gelegenheiten zu defektieren einher. In diesem Zusammenhang ist es wahrscheinlich, dass sowohl Große Menschenaffen als auch Menschen mit Interessenkonflikten konfrontiert sind, wenn sie entscheiden müssen, ob sie mit anderen Gruppenmitgliedern kooperieren. Wenn zum Beispiel eine Gruppe von Schimpansen eine Jagd beginnt, könnte es sein, dass manche Gruppenmitglieder es bevorzugen, zurückzubleiben und darauf zu warten, dass andere Schimpansen die Kosten der Jagd tragen. Indem wir Schimpansen, Bonobos und fünfjährige Kinder jeweils paarweise mit Interessenkonflikten konfrontieren, können wir die Strategien untersuchen, die diese Arten benutzen, um ihr Verhalten in Konfliktsituationen miteinander zu koordinieren und den Konflikt zu überwinden. Durch diesen Artvergleich gewinnen wir Einblicke in die Evolution der menschlichen Kooperation.

Im ersten Kapitel der Dissertation präsentiere ich eine Studie, in der ich Schimpansen paarweise mit einer Konfliktsituation konfrontiert habe, die dem so genannten "Snowdrift Game" entspricht (Studie 1). Dieses Modell aus der Spieltheorie wird dazu benutzt, zu untersuchen, ob Individuen miteinander kooperieren, wenn ihre Interessen miteinander im Konflikt stehen. In diesem Spiel können die zwei Spieler entweder kooperieren oder von der Arbeit des anderen profitieren, ohne selbst etwas beizutragen. Beiderseitige Kooperation wird höher belohnt als beiderseitiges Defektieren. Jedoch ist ein Kernelement dieses Spiels, dass es besser ist zu defektieren, wenn der Partner kooperiert, und zu kooperieren, wenn der Partner defektiert. Mit anderen Worten, es ist besser, das Gegenteil von dem zu tun, was der Partner macht. Um auf das Beispiel der Jagd bei den Schimpansen zurückzukommen: Wenn ein Gruppenmitglied die Jagd startet, können die anderen davon profitieren, ohne selbst aktiv teilzunehmen und die Kosten zu tragen. Wenn jedoch niemand die Jagd startet, hat niemand eine Chance an die Beute zu kommen. Das Dilemma in dieser Situation besteht für die Individuen darin, ob sie die Jagd starten sollen oder nicht, angenommen, dass alle verlieren, wenn niemand die Jagd einleitet. Um die Anreizstruktur dieses Spiels nachzubilden, habe ich Schimpansen paarweise mit einer beschwerten Plattform konfrontiert, auf der sich Belohnungen für beide Individuen befanden. Die Schimpansen mussten entscheiden, ob sie kollaborieren (das heißt, die Plattform zusammen

heranziehen und die Kosten teilen) oder alleine ziehen und die Kosten für die Kooperation alleine tragen. Die Schimpansen hatten eine begrenzte Zeit zur Verfügung, um ihre Entscheidungen zu treffen, bevor ihre Belohnungen verschwanden. Wenn die Kosten für die Kooperation hoch waren, war es die beste Strategie für ein Individuum zu warten, bis der Partner zog und dann die Belohnung zu erhalten, was eine Maximierung der Vorteile bei einer gleichzeitigen Minimierung der Kosten darstellte. Die Leistung der Schimpansen bei hohen Kooperationskosten wurde mit ihrer Leistung in einer Bedingung mit wenig Gewicht verglichen, in der die Kooperationskosten minimal waren.

Die Ergebnisse zeigten, dass Schimpansen erfolgreich ihr Verhalten miteinander koordinierten, um den Konflikt zu beseitigen, und dabei in den meisten Fällen die Belohnungen erhielten. Überraschenderweise kollaborierten Schimpansen häufiger, wenn die Kosten hoch waren, obwohl sie defektieren hätten können. Sie haben allerdings nicht nur kollaboriert, um die Belohnungen zu erhalten, sondern sie zeigten auch klare Anzeichen von strategischen Entscheidungen zur Kostenreduktion. Bei hohen Kosten warteten die Schimpansen länger, bevor sie am Seil zogen, was die Wahrscheinlichkeit reduzierte, alle Kosten alleine zu tragen. Bei einer genaueren Betrachtung der Kollaboration innerhalb der Paare zeigte sich, dass die Individuen ungleich viel Arbeit zum Ergebnis beitrugen. Dies deutet darauf hin, dass sie versucht haben, die Kosten zu reduzieren. Alles in allem weisen diese Ergebnisse darauf hin, dass Schimpansen dazu fähig sind, zwischen erfolgreicher Koordination (innerhalb eines Zeitlimits) und einer Beschränkung der eigenen Kosten auf ein Minimum abzuwägen.

Im zweiten Kapitel der Dissertation präsentiere ich eine Studie, in der ich Bonobos und Schimpansen (Studie 2a) und Kinder (Studie 2b) jeweils paarweise mit einer zweiten Version des „Snowdrift Game“ konfrontiert habe. Im Gegensatz zu der vorherigen Version konnten die Individuen in dieser Version des Spiels nicht innerhalb der einzelnen Durchgänge kollaborieren. Jedoch konnten sie andere Strategien anwenden, um den Konflikt im Verlauf der Studie aufzulösen (zum Beispiel sich abwechseln über die Durchgänge hinweg). Ich habe die drei Arten mit einer rotierenden Plattform konfrontiert, die mit einer ungleichmäßigen Belohnungsstruktur versehen war. Zwei lösbare Seile waren an den beiden inneren Enden der Plattform befestigt. Die Seile verliefen gegenläufig zueinander und jeweils eins führte in die Räume der zwei Testteilnehmer. Jedes Individuum konnte an seinem Seil ziehen, um das innere Ende der Plattform in seine Richtung zu drehen, während gleichzeitig das äußere Ende der Plattform sich zum Partner bewegte. Wenn hingegen beide Individuen zur gleichen Zeit zogen, konnten sich die Seile von der Plattform lösen, so dass keiner einen Zugang zu den Belohnungen erhielt. In der „Snowdrift“-Bedingung war die bevorzugte Belohnung auf dem äußeren Ende positioniert. Sie konnte nur erreicht werden, wenn man darauf wartete, dass der Partner vor einem

am Seil zog. Im Gegensatz dazu war die bevorzugte Belohnung in der kompetitiven Bedingung auf dem inneren Ende gelegen. In dieser zweiten Bedingung war es besser, vor dem Partner zu ziehen. Wie in der vorangegangenen Studie gab es für die Affen und Kinder ein Zeitlimit, in dem sie eine Entscheidung treffen mussten. Das Hauptziel dieser Studie war es, zu untersuchen, ob sich die Individuen in dieser Version des Spiels strategisch verhalten würden, das heißt, ob sie in der „Snowdrift“-Bedingung länger warten würden als in der kompetitiven Bedingung. Ein weiteres Ziel dieser Studie lag darin, die Strategien zu vergleichen, die die drei Arten zur Konfliktbewältigung anwendeten, und zu untersuchen, inwieweit Kommunikation eine bedeutsame Rolle in ihrem Vorgehen spielte.

Die Ergebnisse der Studie zeigten, dass die drei Arten sich jeweils erfolgreich koordinierten und die Belohnungen in den meisten Fällen erhielten. In der kritischen Bedingung haben alle drei Arten länger mit dem Ziehen gewartet, was auf generelles Verständnis der Aufgabe hinweist. Eine Analyse ihrer Zieh-Strategien zeigt, dass Kinder über die Sitzungen hinweg gelernt haben länger zu warten, obwohl sie in den meisten Durchgängen letztlich gezogen haben. Im Gegensatz dazu neigten die Großen Menschenaffen dazu, eine Strategie anzuwenden, bei der nur ein Individuum die meiste Zeit über zog, sowohl bei der „Snowdrift“-Bedingung als auch bei der kompetitiven Bedingung. Jedoch wendeten nicht alle Menschenaffen diese Strategie an; einige Individuen verhielten sich klar strategisch und zogen signifikant häufiger in der kompetitiven als in der „Snowdrift“-Bedingung. Bei der Untersuchung der Frage, ob Affen und Kinder kommunikative Akte verwendeten, um die Koordination zu erleichtern, zeigte sich, dass nur die Kinder während der Aufgabe kommunizierten. Sie benutzten spezifische Arten verbaler Kommunikation, um die Entscheidung des Partners zu ihren eigenen Gunsten zu beeinflussen.

Aufgrund der Strategien, die einige Große Menschenaffen im ersten Teil der Studie zeigten, habe ich einen Folgetest entwickelt, um die Entscheidungsstrategien von Schimpansen und Bonobos detaillierter zu untersuchen (Studie 3). Zu diesem Zweck habe ich die Tiere mit derselben rotierenden Plattform konfrontiert, die im ersten Teil der Studie verwendet wurde (die soziale Option), mit dem Zusatz einer sicheren Belohnung für die beiden Tiere (die nicht-soziale Option). Individuen konnten in diesem neuen Zusammenhang entscheiden, ob sie an dem sozialen Dilemma teilnehmen wollen oder ob sie die nicht-soziale Option wählen. Es war nun nicht mehr möglich, inaktiv zu bleiben. Ein wichtiger Punkt ist, dass die Menge der Belohnungen in der nicht-sozialen Option über die Sitzungen hinweg variierte. Meiner Hypothese nach würde das Hinzufügen der nicht-sozialen Option den Tieren erlauben, die Risiken besser einzuschätzen und strategisch zu wählen, nämlich abhängig von der Verteilung der Belohnungen und der voraussichtlichen Wahl des Partners. Durch meinen direkten Vergleich von Schimpansen und Bonobos konnte ich untersuchen, wie empfindsam die beiden Arten gegenüber einem sozialen Risiko sind in einer Situation, in der dieses Risiko durch das Wählen der

nicht-sozialen Option umgangen werden konnte. Schließlich habe ich erforscht, ob Individuen das vorangegangene Verhalten ihres Partners zu ihrem eigenen Vorteil nutzen würden, um ihre Belohnungen zu maximieren.

Die Ergebnisse dieser Studie zeigten, dass beide Menschenaffenarten sich koordiniert haben, um in den meisten Durchgängen an die Belohnungen zu kommen, und dass sie sich strategisch verhalten haben. Die Latenzzeiten, um an die Belohnungen zu kommen, verringerten sich, wenn die Menge der Belohnungen in der nicht-sozialen Option erhöht wurde. Bei der Wahl der sozialen Option warteten die Affen in der kritischen Bedingung immer noch länger, denn die bevorzugte Belohnung konnte nur erlangt werden, wenn der Partner vor einem zog. Beide Menschenaffenarten wählten die nicht-soziale Option häufiger, wenn sich das Verhältnis der Belohnungen in der nicht-sozialen und der sozialen Option zu Gunsten der nicht-sozialen Option erhöhte. Dies deutet darauf hin, dass Schimpansen und Bonobos keinen signifikanten Unterschied bezüglich ihrer Empfindsamkeit für soziales Risiko aufweisen. Abschließend habe ich herausgefunden, dass Große Menschenaffen ihre Entscheidungen so anpassen, dass sie die Belohnungen maximieren, indem sie kompetitiven Situationen ausweichen und mögliche Entscheidungen des Partners vorhersehen.

Im letzten Kapitel der Dissertation präsentiere ich eine Studie, in der ich Schimpansen (Studie 4a) und Kinder (Studie 4b) jeweils paarweise mit einer Situation konfrontiert habe, die einem Gefangenen-Dilemma („Prisoners' Dilemma“) entspricht. Im Gegensatz zum „Snowdrift Game“ gelangt der Kooperierende beim Gefangenen-Dilemma bei einseitiger Kooperation zum schlechtesten Ergebnis; Individuen profitieren nicht von ihrem einseitigen Handeln. Um das Gefangenen-Dilemma abzubilden, habe ich die Paare mit einer vertikal beweglichen Plattform konfrontiert, die an den Enden mit Belohnungen versehen wurde. Jeder Teilnehmer konnte an einem Seil ziehen, das mit einer Seite der Plattform verbunden war. In der Gefangenen-Dilemma-Bedingung mussten die Teilnehmer warten, bis der Partner kooperiert (das heißt, an dem Seil zieht), um an die bevorzugte Belohnung zu kommen. Im Gegensatz dazu konnten die Belohnungen in der kompetitiven Bedingung nur erreicht werden, wenn man vor seinem Partner zog. Diese Bedingung diente als Kontrolle. Zudem konnten die beiden Individuen in beiden Bedingungen kollaborieren (das heißt, an den beiden Seilen zur gleichen Zeit ziehen) und ihre Belohnungen teilen. Wie bereits in den vorangegangenen Studien hatten die Individuen ein Zeitlimit, um an die Belohnungen auf der Plattform zu gelangen.

Das Hauptziel dieser vergleichenden Studie war es, zu untersuchen, ob Schimpansen und Kinder sich strategisch verhalten würden, um den präsentierten Konflikt zu überwinden. Meiner Hypothese nach würden sich Individuen in diesem Kontext strategischer verhalten als in einer „Snowdrift“-Situation, weil einseitige Kooperation in diesem Fall zu keiner Belohnung für den Kooperierenden führte. Ein



zweites Ziel der Studie war es, die Strategien zu erforschen, die Individuen zur Konfliktüberwindung benutzen, wenn eine Kollaboration möglich ist. Bei den Kindern war ich zudem an der Rolle interessiert, die Kommunikation bei der Aufrechterhaltung einer erfolgreichen Koordination in diesem Gefangenen-Dilemma-Szenario einnimmt.

Die Befunde dieser vergleichenden Studie wiesen darauf hin, dass sich beide Arten substantiell voneinander darin unterschieden, welche Strategien sie zur Lösung der Aufgabe wählten. Schimpansen lernten sich über den Verlauf der Studie strategischer zu verhalten; in der kompetitiven Bedingung zogen sie sehr schnell im Vergleich zu der Gefangenen-Dilemma-Bedingung, in der ihre Latenzzeiten sich erhöhten. Doch letztlich zogen die Schimpansen auch in dieser Bedingung. Eine mögliche Erklärung für dieses hohe Maß an Kooperation könnte sein, dass die Schimpansen versucht haben, ihren Partner zum Ziehen zu verleiten. Dies verwandelte die Gefangenen-Dilemma-Durchgänge in kompetitive Durchgänge, wodurch die Wahrscheinlichkeit für die Schimpansen erhöht wurde, an die Belohnungen zu kommen. Kinder entwickelten eine effizientere Strategie, die darin bestand, sich abzuwechseln, um die Belohnungen alternierend zu erhalten. Interessanterweise haben sie diese Strategie in beiden Bedingungen angewandt. Diesem Befund entsprechend wurden sie schneller im Verlauf der Studie; sobald die Strategie sich abzuwechseln einmal etabliert war, haben sie weniger lange auf die Entscheidung des Partners gewartet. Schließlich habe ich herausgefunden, dass Kinder spezifische Kommunikationsarten benutzt haben, um sich mit ihren Partnern zu koordinieren. Durch diese strategische Kommunikation konnten sie ein hohes Maß an Kooperation in beiden Bedingungen aufrechterhalten.

Durch die Verwendung des "Snowdrift"- und des Gefangenen-Dilemma-Modells konnten wir unser Verständnis bezüglich der Fähigkeiten von Schimpansen, Bonobos und Kindern vertiefen, sich in Situationen zu koordinieren, in denen Interessenkonflikte bestehen. Die Ergebnisse meiner Studien haben gezeigt, dass diese drei Arten verschiedene Konfliktsituationen erfolgreich lösen konnten, besonders, wenn ihr eigenes Handeln zu einem direkten Vorteil für sie führte. Zudem unterstützen die Ergebnisse die Annahme, dass Kinder einzigartige kognitive Fähigkeiten zur Koordination besitzen, was es ihnen erlaubt, effizientere Strategien zu entwickeln, um Konfliktsituationen zu bewältigen.

## **CURRICULUM VITAE**

Alejandro Sánchez Amaro

06.01.1988

Sant Cugat del Vallès, Barcelona

### Education:

2013-present

Ph.D student in Biology. Max Planck Institute for Evolutionary Anthropology, Leipzig. Germany.

2011-2013

M.Sc in Primatology, Universitat de Barcelona, Barcelona, Spain.

2006-2010

B.Sc in Biology, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Spain.

## SCIENTIFIC PUBLICATIONS AND PRESENTATIONS

### Publications

**Sánchez-Amaro, A.**, Duguid, S., Call, J., & Tomasello, M. Chimpanzees, bonobos and children successfully coordinate in conflict situations (manuscript under review).

**Sánchez-Amaro, A.**, & Amici, F. (2016). Markets carefully interpreted. A reply on Kaburu, S. S. K. & Newton-Fisher, N. E. (2016). *Animal Behaviour*, *119*, e7-e13.

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### Presentations

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**Sánchez-Amaro, A.**, Peretó, M., & Call, J. "Natural Choices of Food in Great Apes". Talk at 14th Gesellschaft für Primatologie Conference. Leipzig, Germany 2015.

**Sánchez-Amaro, A.**, Duguid, S., Call, J., & Tomasello, M. "Strategic decision-making by chimpanzees in a Snowdrift Game". Talk at 2nd European Student Conference on Behaviour and Cognition. Zurich, Switzerland 2015.

**Sánchez-Amaro, A.**, Duguid, S., Call, J., & Tomasello, M. "Strategic decision-making by chimpanzees and children in a Snowdrift Game". Talk at the European Human Behaviour and Evolution Association (EHBEA) Conference 2015. Helsinki, Finland 2015.

**Sánchez-Amaro, A.**, Peretó, M., & Call, J. "Difference in between-reinforcer value modulate the selective value effect in Great Apes". Talk at Behaviour 2015. Cairns, Australia 2015.

**Sánchez-Amaro, A.**, Duguid, S., Call, J., & Tomasello, M. "Coordination despite conflict in chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and children". Talk at XXVI International Primatological Conference (IPS). Chicago, USA 2016.

## Posters

**Sánchez-Amaro, A.**, Peretó, M., & Call, J. "Natural Choices of Food in Great Apes". Finalist of Student Award Competition. Poster at XXV International Primatological Conference (IPS). Hanoi, Vietnam 2014.

**Sánchez-Amaro, A.**, Duguid, S., Call, J., & Tomasello, M. "Chimpanzees and children strategic decision-making in Snowdrift Games". Poster at Behaviour 2015. Cairns, Australia 2015.

**Sánchez-Amaro, A.**, Duguid, S., Call, J., & Tomasello, M. "Coordination under conflict in chimpanzees (*Pan yroglodytes*), bonobos (*Pan paniscus*) and children". Poster at VIII Conference on Cognitive Science. Dubrovnik, Croatia 2016.

**Sánchez-Amaro, A.**, Duguid, S., Call, J., & Tomasello, M. "Strategic decision-making by chimpanzees (*Pan Troglodytes*), bonobos (*Pan Paniscus*) and children in a Snowdrift-Game task". Poster at Chimpanzees in Context Symposium. Chicago, USA 2016. Electronic Poster.

## **ERKLÄRUNG GEMÄß §8(2) DER PROMOTIONSORDNUNG**

Hiermit erkläre ich, Alejandro Sánchez Amaro, geboren am 06.01.1988, Sant Cugat del Vallès, España, die vorliegende Dissertation selbständig verfasst und dabei keine anderen als die angegebenen Quellen oder Hilfsmittel verwendet zu haben.

Bei der Durchführung und Auswertung der in dieser Arbeit erwähnten Studien waren Michael Tomasello, Josep Call and Shona Duguid beteiligt.

Außer den oben genannten Personen waren keine weiteren Personen an der geistigen Herstellung der vorliegenden Arbeit beteiligt. Die Hilfe eines Promotionsberaters habe ich nicht in Anspruch genommen. Dritte haben weder mittelbar noch unmittelbar geldwerte Leistungen von mir erhalten, die in Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Die vorgelegte Arbeit wurde bislang weder veröffentlicht, noch in gleicher oder ähnlicher Form einer anderen wissenschaftlichen Einrichtung zum Zwecke einer Promotion oder eines anderen Prüfungsverfahrens vorgelegt.

Leipzig, am 24.04.2017

