1

2 Social manipulation in nonhuman primates: cognitive and motivational determinants

3 C. J. Völter[a, b*], F. Rossano[c], & J. Call[a, b]

4

5 [a] School of Psychology and Neuroscience, University of St Andrews, St Andrews, UK

6 [b] Department of Developmental and Comparative Psychology, Max Planck Institute for

7 Evolutionary Anthropology, Leipzig, Germany

8 [c] Department of Cognitive Science, University of California, San Diego, USA

9

10

11

12

13 *Correspondence:

14 Christoph J. Völter

15 University of St Andrews

16 School of Psychology & Neuroscience

17 Westburn Lane

18 St Andrews

19 Fife

20 United Kingdom

21 Email: christoph.voelter@gmail.com

22 Phone: + 49 341 3550 450

23

1   Abstract

2   Social interactions are the result of individuals' cooperative and competitive tendencies

3   expressed over an extended period of time. Although social manipulation, i.e., using another

4   individual to achieve one's own goals, is a crucial aspect of social interactions, there has been

5   no comprehensive attempt to differentiate its various types and to map its cognitive and

6   motivational determinants. For this purpose, we survey in this article the experimental

7   literature on social interactions in nonhuman primates. We take social manipulation,

8   illustrated by a case study with orangutans (*Pongo abelii*), as our starting point and move in

9   two directions. First, we will focus on a flexibility / sociality axis that includes technical

10   problem solving, social tool-use and communication. Second, we will focus on a motivational

11   / prosociality axis that includes exploitation, cooperation, and helping. Combined, the two

12   axes offer a way to capture a broad range of social interactions performed by human and

13   nonhuman primates.

14

15

16   Keywords

19

1. Introduction

In the last 20 years two major lines of research on the social psychology of nonhuman primates developed, one on cooperation and helping, and one on theory of mind and deception. Whereas the literature on cooperation focused mainly on the underlying motivation of the cooperators, the theory of mind literature focused on the cognitive nature of the underlying representations. It has recently been proposed that these two lines of research need to be re-aligned (Schmelz and Call, 2016). This re-alignment requires, first, to examine whether nonhuman animals are also sensitive to the perspectives, knowledge states, and beliefs of their cooperators, and second, to dissect the cognitive processes involved in cooperating with others (see also Albiach-Serrano, 2015).

Social interactions are relevant in many contexts and depend to a large degree on the socio-ecology of a species. Differences in social interactions might be accompanied by variations in socio-cognitive abilities. Primates are a diverse taxonomic group characterized by a broad range of socioecological lifestyles. Cooperative interactions in primates, for example, have many manifestations such as grooming, pair bonding, group hunting, or agonistic support. Notwithstanding the manifold contexts and manifestations of social interactions, we will focus here on experimental studies aiming at cooperative and competitive problem solving. We focus on these studies because the immediate payoffs that result from social interactions, the ways animals can coordinate their actions with each other (e.g., physical interactions, communication), and the temporal extent of these interactions (trial duration and number) can be measured or even manipulated. Even though most of the reviewed studies focus on prosocial tendencies and coordination, they also allow us to assess primates' selfish and manipulative strategies.

1 Various definitions of social interactions have been used in the literature. Noë (2006)

2 proposed that cooperation and social interactions more generally can be classified along

3 different dimensions including form, outcome, and temporal extent. Form-based definitions

4 are informative about the social nature and specificity of the strategies that individuals are

5 adopting. Noë distinguished between instrumental cooperation and communicative

6 cooperation. Instrumental cooperation encompasses instances in which two animals

7 simultaneously try to solve a problem without necessarily taking the role of the partner into

8 account. Communicative cooperation refers to situations in which animals coordinate their

9 actions by communicating with each other. By definition, communicative cooperation

10 involves social interactions (rather than incidental co-acting) and greatly benefits from some

11 basic capacity for goal understanding. Outcome-focused definitions define social interactions

12 in terms of the payoff that each individual receives following a social interaction. The

13 temporal dimension of social interactions is important here. The returns may be immediate or

14 delayed, whereby the extent of the delay feeds back on the value of the outcome (cf. temporal

15 discounting). Repeated interactions expressed over an extended period of time might enable

16 tolerance towards asymmetrical outcomes of single interactions.

17 However, focusing on one dimension only can be misleading. For instance, focusing only on

18 the outcome of an interaction might result in a classification that includes optimal foraging

19 strategies without any social component. This is exemplified by studies that used operant

20 chambers to examine social interactions. Typically, these studies involve two animals, each

21 one in a different operant chamber (e.g., Savage-Rumbaugh et al., 1978; Stephens et al.,

22 2002). Following individual training, the animals make decisions in the test that affect not

23 only their own outcome but also the outcome of their 'partner' (i.e. a conspecific in an

24 adjacent compartment). Even if there are control conditions that show that the partner's

25 presence is affecting the subjects' decisions, these studies might be explained by instrumental

learning together with social facilitation effects. Giving subjects the opportunity to interact directly with each other increases the ecological validity of the task and might produce additional evidence supporting the role of socio-cognitive processes in these studies. Focusing on the form of an interaction without considering the outcome, in contrast, must fall short of differentiating between different types of social interactions and their motivational foundation. Food-related motivation, in turn, may be uncovered by manipulating the payoff structure of the problem situation.

For these reasons, we will use two interrelated axes to classify social interactions in nonhuman primates (see Figure 1). The first cognitive axis focuses on flexibility and sociality involved in cooperative problem-solving tasks. It includes technical problem solving, social tool-use and communication. The second axis focuses on motivational aspects that include spite, exploitation, cooperation, and helping. The challenges differ depending on whether the partners' goals are coinciding or in conflict. With coinciding goals, the challenge is to coordinate actions with a partner; conflicting goals might rather afford manipulating others.

In this paper, we review experimental research on the cognitive and motivational processes supporting social interactions of nonhuman primates. We will pay special attention to instances in which nonhuman animals manipulate each other, as these shed light on cognitive as well as motivational aspects of social interactions. On the cognitive side, we will include reports on coercion, harassment, solicitation, and communication in cooperative problem solving situations. On the motivational side, we address (besides cases of self-regard) mechanisms that allow for maintaining cooperation even in situations resulting in unbalanced payoffs like, for instance, delayed reciprocation, trust, and prosociality. Antisocial motives may also be at work during some interactions, in particular when animals are faced with unequal payoffs or labor distribution. However, as we will point out, the presence of antisocial motives is only rarely examined in experimental studies.

We organized the article as follows. First, we present a case study with orangutans that illustrates the interplay between the two axes. Second, we address the question how primates manipulate their conspecifics during social interactions in situations when they can exert physical control over conspecifics but also in cases in which this is not possible. Third, we examine the motivational underpinnings of primates' social interactions. In particular, we look at how they move from exploitation to cooperation and helping. Finally, we end by discussing the relation between the two axes at a proximate and an ultimate level.

2. Cooperation and social tool-use in orangutans: a case study

Social complexity has been suggested to be a driving factor for the evolution of cognitive flexibility in primates. Accordingly, group-living might increase resource competition among group members. Therefore, socio-cognitive abilities that allow for competing with others effectively may follow, in particular, social manipulation, tactical deception and coordination abilities (Byrne and Whiten, 1988; Dunbar, 1998). Few studies, however, directly tested this hypotheses by comparing primate species with different socio-ecological lifestyles in cognitive tasks (with some exceptions, see Amici et al., 2008; MacLean et al., 2008). In particular, more comparative experimental work on cooperation and social manipulation with broader phylogenetic coverage is needed.

Orangutans have a semi-solitary lifestyle. From their current socio-ecology, one would not necessarily expect them to have specialized cognitive abilities and / or prosocial tendencies scaffolding social interactions (at least relative to more gregarious primate species). Studying how orangutans as the least gregarious genus of extant great apes interact with each other when presented with cooperation problems might thus give us an interesting reference point for comparison with group-living primates.

1   We set out to investigate strategies in Sumatran orangutans' (*Pongo abelii*) social interactions

2   by looking at great ape mother-offspring dyads (Völter et al., 2015). To do so, we presented

3   three orangutan mother-offspring dyads as well as one chimpanzee (*Pan troglodytes*) and two

4   bonobo (*Pan paniscus*) mother-offspring dyads with different situations in which we placed a

5   food reward outside their enclosure. All apes lived in stable social groups in Leipzig zoo

6   under similar housing conditions and were raised by their respective mothers (except for the

7   chimpanzee mother who was nursery-raised). Crucially, the offspring (all juveniles were of

8   similar age, M_{Age}=4 years ± 2 months, Völter, Rossano, & Call, 2015, unpublished data),

9   unlike their mothers, could reach the food reward due to their smaller body size. We

10   examined how great ape mothers would react to this situation. We found a striking difference

11   between orangutan and *Pan* mothers. All orangutan mothers not only stole food from their

12   offspring once they had obtained it but they even proactively manipulated their offspring's

13   actions (see below). In contrast, we never observed anything resembling this with our three

14   *Pan* mother-offspring dyads. Chimpanzee and bonobo mothers never stole the food that their

15   offspring had obtained nor did they try to manipulate their offspring physically. The

16   chimpanzee and bonobo juveniles could even retrieve the food and walk over to their

17   mothers, sit on their lap, and eat it without any interference. Given the small sample size, the

18   observed differences between *Pan* and *Pongo* need to be interpreted with caution.

19   Nevertheless, these findings point to interesting differences in mothers' tolerance towards

20   their offspring feeding in their proximity, with greater tolerance in group-living *Pan* species

21   compared to the semi-solitary orangutans. It is possible that the observed difference between

22   orangutans and chimpanzees or bonobos was affected by the species-typical age of weaning.

23   Weaning occurs later in orangutans (at around 7 years of age; van Noordwijk and van Schaik,

24   2005) compared to bonobos and chimpanzees (at around 5 years of age; Pusey, 1983). All

25   juveniles in our study were about 4 years of age and not completely weaned yet. However,

1 *Pan* immatures were presumably already more independent from their mothers with regard to

2 foraging than orangutans. Thus, greater dependence of orangutan juveniles may have

3 promoted their mothers stealing food from them.

4 The orangutan mothers' proactive manipulation of their offspring consisted of actively

5 coercing them into retrieving the food. By carrying their offspring to the locations where the

6 offspring could access the food, pushing their hands and bodies toward the food and pulling

7 them back once they had grabbed the food (see Figure 2 *a* and *b*), orangutan mothers gained

8 access to the food. Crucially, this *social tool-use* depended on their offspring's willingness to

9 complete the required actions (i.e. grabbing the food). That is to say, orangutan mothers could

10 only coerce their infants into performing parts of the solution. Specifically, they could bring

11 their offspring's hands and bodies close to the food but they could not force them to grab the

12 food. Their actions, therefore, resembled physical tool use (e.g. using a stick to rake in an

13 out-of-reach reward) but could not be reduced to it because they had to take the self-

14 controlled actions of the social tool into account.

15 In a follow-up experiment, we extended these findings by showing how orangutan mothers

16 would also coerce their offspring into retrieving a stick tool that they, in turn, required to

17 access a food reward. Next, we were interested in whether orangutans' tendency to use their

18 offspring as a tool to access food and tools would also lead them to cooperate with their

19 offspring if this was necessary to access food. Therefore, we set up a situation in which

20 mothers received the stick tool at the beginning of each trial; however, now only their

21 offspring could access the apparatus where the tool could be used (Völter et al., 2015).

22 Inserting the tool into the apparatus activated a mechanism resulting in the delivery of food

23 rewards for both mother and offspring. The two mothers tested with this setup quickly passed

24 the tool to their offspring (see Figure 2 *c*). One mother actively handed the tool over to her

25 son already in the first trial. The other one let her daughter take the tool from her in the first

trial. After she had seen her daughter inserting the tool in the apparatus in trial 1, she started to actively hand the tool over from the second trial onwards. Interestingly, they would not only pass the tool to the offspring but also actively push them into the direction of the tool-use apparatus, if the offspring was reluctant to go there. In one instance, an orangutan mother only released her son once he had grabbed the tool that she was offering him. Thus, mothers were physically manipulating their offspring even while cooperating with them in order to obtain the desired reward.

As a next step, we looked at whether adult orangutan females would cooperate with each other (Rossano, Völter, & Call, in preparation). We presented three adult orangutans (two of them had participated in previous study) with the same cooperative problem-solving apparatus as before. One individual received the tool but only another individual in the adjacent compartment of the enclosure could insert it into the apparatus. We found that the orangutan females passed the tool spontaneously and reliably to each other and maintained cooperation even when they knew they would not receive food in some trials.

Finally, we were interested in the strategies orangutans would employ when both the potential tool giver and recipient had a visible nonsocial alternative. This nonsocial alternative consisted of a horizontally mounted Plexiglas chute with a food reward inside. By inserting the tool into this chute, the orangutans could push the food reward into a hole, down a ramp, and within their reach. Orangutans passed the tool on to their partner only if they could obtain a higher value food reward by cooperating with the partner. However, as their potential cooperators also had alternative options, passing the tool to the partner did not always lead to the desired outcome. If the partner preferred to use the tool for her nonsocial option, the tool giver would get nothing. Importantly, after having passed the tool, the tool giver could not control the decision of the tool recipient. Nevertheless, orangutans tried to cooperate by passing the tool in an unusual manner (something that they would not do before

1   we added the nonsocial option for the tool recipient). After some experience with the task, all

2   tested orangutans passed the tool sometimes high above their head (see Figure 2 *d*),

3   presumably to influence their partner's choice. The cooperation apparatus (that would release

4   food for both individuals) was mounted close to the ceiling of the enclosure, whereas the

5   nonsocial apparatus was mounted below, near the floor. By passing the tool high, the partner

6   was closer to the social apparatus when receiving the tool. However, their manipulative

7   attempts were not always successful because the tool recipients tended to insert the tool in the

8   apparatus that yielded the highest reward for them and not primarily based on the location

9   where they received the tool.

10   In summary, this series of experiments shows how orangutans flexibly manipulate their

11   conspecifics by physically manipulating their bodies, transferring resources to conspecifics if

12   necessary, and even attempt to exert control in the way they transfer these resources.

13   Orangutans' performance supports the role of social manipulation even within cooperative

14   situations. On the one hand, orangutans' preference for individual foraging suggests that their

15   decisions were predominantly driven by self-regarding motives. It remains to be seen to what

16   extent they can maximize their payoffs by taking the incentives of their partners into account.

17   On the other hand, orangutans were able to maintain cooperation across multiple trials in

18   which they knew they would not receive a reward. The precise mechanisms that allowed

19   them to tolerate unbalanced outcomes over a limited period of time are not clear yet and

20   should be addressed by future research. Importantly, these studies emphasize the need to

21   consider both cognitive and motivational aspects when studying social interactions.

22

23   **3. From technical problem-solving to communication: Cognitive aspects of social**

24   **manipulation**

1 Field studies have provided observational evidence for social manipulations in various

2 primate species. One such phenomenon has been called *agonistic buffering* (Deag and Crook,

3 1971). Here, males use infants and/or females to reduce the likelihood of aggression. During

4 or before potentially aggressive interactions among males, one of the males may pick up an

5 infant or grab a female. Typically, this behavior reduces the agonistic nature of the male-male

6 interaction. Such agonistic buffering has been described, for instance, in olive baboons, *Papio*

7 *anubis* (Strum, 1983, 1984), Barbary macaques, *Macaca sylvana* (Deag and Crook, 1971;

8 Whiten and Rumsey, 1973), and geladas, *Theropithecus gelada* (Dunbar, 1984).

9 The experimental investigation of social manipulation, cooperation, and their psychological

10 underpinnings typically involves tasks that require identical and simultaneous or

11 complementary and sequential actions of usually two individuals. We will address here

12 different cognitive strategies that animals employ to solve these problems. In particular, we

13 differentiate these strategies based on the extent to which they are specific to the social

14 domain and the flexibility they allow for in order to influence the behavior of others.

15 Primates may use their technical knowledge, i.e. their knowledge about causal and physical

16 relations in their environment, also in cooperative problem-solving situations. Instead of

17 paying attention to their partner's actions, animals may focus on the causal effects of their

18 partner's actions. Clear-cut cases of social manipulative strategies in cooperative problem

19 solving involve direct physical and / or communicative interactions between participants.

20 Such manipulative strategies have been termed social tool use (e.g., Bard, 1990; Bullinger et

21 al., 2011a).

22 We have subdivided social tool use previously into different levels depending on the extent to

23 which the tool-user is exerting physical control over the social tool (Völter et al., 2015). This

24 might involve complete or partial physical control, for cases in which the tool user coerces

the social tool physically into executing certain actions. Cases of complete control over the social tool (level 1) are equivalent to physical tool use. For example, a mother pulls back the arm of an infant who grabbed a food reward in order to bring the food within reach, which resembles pulling in a rake to access out of reach food. Partial control (level 2) involves a mixture between coercive behaviors of the tool user and self-controlled and self–initiated actions of the social tool. An example would be a mother guiding her infant's arm toward an otherwise inaccessible food reward. Once the infants arm is close to the reward, the mother needs to wait until the infant has grabbed the food. Making predictions about self-controlled actions of other individuals can be seen as a first indication of a truly social manipulative strategy.

There are also cases of social tool use in the absence of direct physical control. Here, the social tool acts without being physically constrained by the tool-user and social manipulation can work indirectly based on exerting control over certain resources (level 3) or based on communication, for instance, by producing attention-getters or pointing gestures to solicit cooperation from others (level 4). These types of social tool use will depend to a large degree on coinciding goals between the tool-user and the social tool like, for example, in mutualistic settings.

3.1 Technical problem solving

Many primate species are known as innovative and flexible problem-solvers (for recent reviews on individual problem-solving, see Seed and Mayer, in press; Völter and Call, in press). Innovation and tool-use rates are positively correlated in the primate clade with great apes and brown capuchin monkeys showing the highest performance (Lefebvre et al., 2004). These tool-using species select tools flexibly with respect to functional properties of the tools depending on the problem situation they are currently encountering. For example, apes and

capuchin monkeys select tools based on their length, rigidity, pliability, or weight depending on the task, often spontaneously without the opportunity for reinforcement learning over many trials (e.g., Manrique et al., 2010; Manrique et al., 2011; Mulcahy et al., 2005; Schrauf and Call, 2011; Schrauf et al., 2012). In contrast, their understanding of other object properties such as connectivity or support is less clear (e.g., Fujita et al., 2003; Herrmann et al., 2008; Povinelli, 2000). In any case, the point here is that primates may use their technical problem-solving abilities also in cooperative problem-solving tasks.

In the cooperation literature, two main paradigms have been used to investigate nonhuman primates' ability to work together: string-pulling tasks with identical roles and tool transfer tasks with complementary roles. Cooperative string-pulling tasks come in two variants; both require that two individuals pull at a string simultaneously to bring food rewards into reach. The degree to which the individuals need to synchronize their actions at the beginning of each trial differs, however. In the first variant, two individuals need to pull in a box that is too heavy for one individual alone (e.g., Crawford, 1937; Povinelli and O'Neill, 2000), or alternatively, two individuals need to pull two ropes simultaneously that are connected to a food dispensing mechanism (e.g., Chalmeau, 1994; Chalmeau et al., 1997a). The second variant is the loose string paradigm, which appears causally more transparent. Here, two individuals need to pull the two ends of a long rope simultaneously in order bring baited platforms within reach (e.g., Hirata and Fuwa, 2007). The rope is only loosely connected with the baited platform. If only one individual is pulling the rope, the other end of the rope will move out of reach and the food is lost for both individuals. Therefore, both variants require temporal synchronization of the actions but in the loose string variant individual pulling invariably results in the loss of food.

As mentioned before, studies on individual string pulling have shown a limited understanding of connectivity and support in nonhuman primates (e.g., Fujita et al., 2003; Herrmann et al.,

2008; Povinelli, 2000). This is problematic for cooperation studies building to some extent on the assumption that subjects understand how the string pulling apparatus works. Notably, the string pulling setups used in cooperation studies are usually more complex than the ones used in individual string pulling. It is therefore unsurprising that most of the cooperative apparatus problems required extensive experience with the task-relevant contingencies. In some studies subjects required extensive training already at the stage of individual familiarization with the task (e.g., Chalmeau and Gallo, 1993). In other studies, subjects required extensive experience before entering the critical test phase. In the critical test phase of the loose string paradigm, for instance, the arrival of the partner at the apparatus is delayed. Therefore, the subject needs to wait for the partner to arrive before pulling in the rope. Chimpanzees in the original study by Hirata and Fuwa (2007) received more than 500 trials without a delay before they entered this delay condition. Other studies with the same paradigm did not use a training procedure and found that some chimpanzee dyads succeeded spontaneously in this cooperation task but they also relaxed the requirement for pulling simultaneously by making the rope longer (Melis et al., 2006b, c).

Subjects may succeed in the delay condition by learning to take the role of their partner into account. However, other explanations do not require any attention to the role of the partner. For example, subjects may learn to pull the string only if they feel tension at the string, which is usually only the case when the partner is holding the opposite end of the string. Alternatively, they might synchronize to an external event such as the door opening or the behavior of the human experimenter that signals the arrival of the partner. In one of the first experimental studies on cooperation, chimpanzees were explicitly trained to pull simultaneously in response to a verbal command by the experimenter (Crawford, 1937). Hirata and Fuwa (2007) also noted that chimpanzees were synchronizing their actions to the experimenter stepping aside at the beginning of the trial. Moreover, sometimes a shaping

procedure is used in the delay, gradually increasing the delay of the partner's arrival, which makes operant conditioning more likely (Melis et al., 2006b).

One might argue that domain-general strategies such as instrumental learning would not predict large species differences in this task. Some species (e.g., *Pan troglodytes*, Hirata and Fuwa, 2007; *Elephas maximus*, Plotnik et al., 2011) learned to wait for the partner in the loose string paradigm, while others did not (*Corvus corax*, Massen et al., 2015; *Canis familiaris*, Ostojić and Clayton, 2014; *Psittacus erithacus*, Péron et al., 2011; *Corvus frugilegus*, Seed et al., 2008). However, obvious factors that might contribute to the failure of some species in the delay conditions are interspecies differences in inhibitory control and / or physical understanding of the task.

Other cooperation or helping studies involved sequential actions. In these studies, usually two individuals were located in separate but adjacent compartments. One individual receives one or multiple tools (the tool giver) but only the partner (the tool user) can use one of the tools. Again, subjects might just learn over trials that they need to pass the tool to the adjacent cage, which will result in a food reward for both. Thus, it is possible that subjects solve these tasks without taking the role of the partner into account. Looking at the way subjects pass the tool (e.g. passing the tool directly to the partner) and communication between partners (e.g. begging gestures by the tool recipient) may be informative here. Sometimes the tool giver has multiple potential tools available (functional and non-functional ones). Selective tool transfer has been considered as evidence that individuals know what their partner needs (Yamamoto et al., 2012). However, usually subjects received an individual training phase before entering the dyadic test phase. In the training, subjects might have learned to prefer certain tools to others in certain contexts. Alternatively, they might pass on the object that they themselves cannot use currently (Melis and Tomasello, 2013; Yamamoto et al., 2009).

Future studies should address these issues by examining how quickly apes can learn to

synchronize their behavior with a nonsocial event, which is as salient as a conspecific (see

Heyes, 2015, for a similar criticism on the theory of mind literature). Likewise, in the

sequential action paradigms studies might explore whether subjects would learn at equal rates

to pass the tool to an empty compartment given the same reinforcement schedule and stimuli

that attract their attention to a similar extent compared to a conspecific. Moreover, studies

should address other nonsocial strategies such as whether apes in the loose string paradigm

are merely sensitive to the tension at the rope when they are apparently waiting for their

partner to arrive.

3.2 Coercive interactions

Coercing another individual into performing certain actions is costly due to physical demands

associated with it and because it can result in conflicts with the target individual and other

group members. A power differential between the interactants is a prerequisite for coercion to

occur. However, power differential is also related to low tolerance between group members.

Low tolerance, in turn, has been identified as one of the factors limiting the occurrence of

cooperation in non-human primates (Melis et al., 2006c; Petit et al., 1992; Werdenich and

Huber, 2002). This is probably also why most coercive interactions that have been described

in the literature during instrumental cooperation tasks occurred between adults and infants or

juveniles. Adult-offspring relationships often combine high tolerance with a marked power

differential between individuals.

In a tool-use study with Japanese macaques (*Macaca fuscata*) that required the monkeys to

use stick tools or stones to extract a piece of food from a horizontal tube, three females used

their infants as tools to retrieve the reward (Tokida et al., 1994). Once the infants had climbed

into the tube by themselves and bit the apple, their mothers pulled them back and took the

food from them (level 1 social tool-use). One female took this one step further by taking

action before the infants made contact with the food. Not only did she pull her infants back

once they bit the apple but she brought them to the tube and pushed them inside it to begin

with (level 2). Over the course of time, she used all of her four infants in this way as social

tools. When we presented orangutan (*Pongo abelii*) mother-offspring dyads with comparable

problem situations, in which only the offspring could access pieces of food, orangutan

mothers displayed similar behaviors (Völter et al., 2015). Orangutan mothers dragged the

offspring to the site where they could access the food, guided their arms and bodies towards

the food, and pulled them back once the juveniles grabbed the food.

Chalmeau (1994) reported in the context of the cooperative string-pulling task that a

dominant chimpanzee repeatedly caught a juvenile with whom he had been working together

before. He then carried the juvenile to the string-pulling site. However, the juvenile was often

unwilling to pull the string after the adult had caught her and escaped towards her mother.

The adult subsequently adopted a waiting strategy, by staying near the apparatus until the

juvenile approached it voluntarily. Similarly, when the same task was presented to two

subadult orangutans (*Pongo pygmaeus*), one of them repeatedly pushed his partner toward

one of the strings and waited until the latter pulled in the string (Chalmeau et al., 1997a).

Instances of coercive social tool use have also been reported outside the primate clade. In an

instrumental cooperation study with keas (*Nestor notabilis*), one individual had to operate a

lever at one end of a seesaw-like apparatus for her partner to extract a food reward from a box

underneath the other end of the seesaw (Tebbich et al., 1996). Presented with this task, three

individuals aggressively approached subordinate partners until they would operate the lever,

which allowed the dominant birds to access the food. In this way, the dominant individuals

were enforcing cooperation. There is anecdotal evidence for coercive social tool use in

elephants (Chevalier-Skolnikoff and Liska, 1993): large bulls were observed to push younger

1 ones against fences, which resulted in the fences breaking and allowing the elephants to pass

2 through.

3 *3.3 Control via access to resources*

4 An animal might exert control during social interactions by controlling access to a feeding

5 site or other task-relevant components (such as tools). In sequential-action cooperation

6 problems, a tool is given to the subject who cannot use it because the tool use location is in

7 the adjacent compartment of the enclosure inaccessible to the subject. The solution is to pass

8 the tool to a conspecific in the adjacent compartment who can use the tool. Passing the tool

9 may, depending on the study, result in a food reward for both individuals (mutualism) or only

10 for one of them (helping).

11 When chimpanzee dyads in adjacent compartments were presented with a mutual helping

12 situation in which each chimpanzee required the tool of the other one to access food

13 (Yamamoto et al., 2009), chimpanzees exchanged tools most of the time upon request (see

14 section 3.4 on communication below). However, sometimes they also exchanged tools in the

15 absence of such requests.

16 In another variant of the tool transfer paradigm, chimpanzees were presented with an

17 apparatus that required the use of two different tools from different sides of the apparatus

18 (Melis and Tomasello, 2013). During the training, the chimpanzees learned to use both tools

19 in sequence to extract food rewards. In the cooperation test phase, subjects could only access

20 one side of the apparatus. The other side of it was accessible to another chimpanzee in the

21 adjacent enclosure. The subject then received both tools. Ten out of 12 chimpanzees

22 transferred tools to their partner and they tended to transfer the tool that their partner would

23 need to operate her/his side of the apparatus. There was considerable variation in the onset of

24 tool transfer but three of the chimpanzee started to pass the tool from the first trial onwards

1   (but they had experience with passing tools in a pilot experiment several months before the

2   test). These findings raise the possibility that chimpanzees use conspecifics as social tools to

3   complete an action they cannot do by themselves by supplying them with the task-relevant

4   resources. Likewise, orangutans were adept at transferring tools to their partners (their

5   offspring and kin and non-kin adults) on the basis of individual training with the task (Völter

6   et al., 2015; Rossano et al., unpublished data). Additionally, in a token transfer task,

7   orangutans, but not chimpanzees, bonobos, or gorillas, consistently exchanged tokens that

8   were valuable only for their partners (Dufour et al., 2009; Pelé et al., 2009).

9

10   *3.4 Communication: soliciting behaviors and requests*

11   Crawford (1937) reported that two of five young chimpanzees that were trained on the

12   cooperative string-pulling paradigm showed solicitation behaviors when their partner lost

13   motivation and stopped pulling in the baited box. Crawford described sequences of behaviors

14   that include leaving the rope and approaching the partner, producing begging gestures,

15   whimpering, touching and pulling the partner on the shoulder, arm, and neck, returning to the

16   string location, and looking toward the partner. If the partner was not responding by starting

17   to pull the rope, these behaviors were sometimes repeated until the partner began to

18   cooperate. Crawford noted that "often only after persistent solicitation did the partner take his

19   rope and begin to pull" (p. 67). Once they showed these solicitation behaviors, they also used

20   them with other partners. Crawford (1941) found such solicitation behaviors also in two

21   adolescent chimpanzees with another cooperative problem-solving task involving sequential

22   and complementary responses.

23   Although Povinelli & O'Neill (2000) agreed that these solicitation behaviors might show that

24   chimpanzees can manipulate each other's behavior, they were skeptical whether chimpanzees

were using these behaviors deliberately to influence the intentions of their partner. Given that these behaviors only occurred after extensive training, Povinelli and O'Neill (2000) argued, it appears plausible that certain behaviors (that were part of their behavioral repertoire) were conventionalized by means of the reinforcement regime of the study, which resulted in the observed solicitation behaviors. In line with this notion, Crawford (1937) stated that "the solicited animal did not seem to know what to do, and only after trying a number of responses under continued solicitation, was the pulling-in behavior given, after which solicitation ceased" (p. 68).

Using Crawford's box-pulling task, Povinelli and O'Neill (2000) paired experienced chimpanzees that were trained to pull in the box together with naïve chimpanzees. In contrast, to Crawford's results they did not find any evidence for physical or communicative manipulations by the experienced individuals compared to the naïve ones. In contrast to Crawford's study, however, chimpanzees in Povinelli and O'Neill's study received only two sessions per dyad.

In line with the latter findings, Hirata and Fuwa (2007) and Melis and colleagues (2006c) found no soliciting behavior between chimpanzees in the loose string paradigm either. However, one chimpanzee showed soliciting behavior toward human partners (Hirata and Fuwa, 2007). When the human partner's arrival at the apparatus was delayed by two seconds, the chimpanzee first failed to retrieve the food multiple times. After having failed seven times, the chimpanzee showed solicitation behavior by looking up at the experimenter's face, whimpering, and taking his hand. In response to the chimpanzee taking his hand, the experimenter approached and operated the apparatus together with the chimpanzee. From this trial onwards, the chimpanzee showed soliciting behavior towards the human partner in most trials. However, when subsequently paired with a chimpanzee again, no soliciting behavior was observed. Soliciting behaviors by chimpanzees and a gorilla toward humans have been

1 reported before (Gómez, 1990; Köhler, 1925). Gómez, for example, described an episode in

2 which an infant gorilla (*Gorilla gorilla gorilla*) took the hand of a human, guided him to a

3 locked door, and placed his hand on the latch, which was interpreted as solicitation to open

4 the door. Warneken and colleagues (2006), in contrast, did not find any evidence that juvenile

5 chimpanzees would try to reengage a human partner after the latter had stopped participating

6 in a cooperative activity.

7 Melis et al (2006b) investigated whether chimpanzees would recruit the most skillful partner

8 in the loose string paradigm. After some training with individual string-pulling, the delay

9 condition that required them to wait for the partner, and training with a door mechanism,

10 chimpanzees learned to open the door to recruit the most skillful cooperator (based on past

11 cooperative experiences). However, as the authors reported, the most skillful partners were

12 also more likely to sit in front of their respective door and to produce noises by shaking the

13 door. Therefore, chimpanzees' partner choice might have been at least partially driven by

14 attention-getting behaviors by the most motivated partner.

15 In another implementation of the loose string paradigm, two chimpanzees started with an

16 individual foraging situation (Bullinger et al., 2011b; Duguid et al., 2014). At some point,

17 they could both switch to the cooperative string pulling apparatus, which - if both decided on

18 it - would lead to a higher value food reward for each chimpanzee (the studies were

19 instantiating Rousseau's Stag Hunt game). If only one individual decided on the cooperative

20 option (i.e. the stag) by leaving the individual foraging option (i.e. the hare), she would lose

21 both foraging options. Therefore, leaving the individual foraging site was a risky strategy.

22 Chimpanzees coordinated their actions by using a leader-follower strategy. In about 10% of

23 the trials, the leaders (i.e. the chimpanzee that was first to arrive at the cooperative string-

24 pulling apparatus) produced attention-getting behaviors such as clapping, banging against the

25 mesh, and they vocalized when they were already at the cooperative option waiting for their

1 partner. However, chimpanzees (in contrast to human children) never reduced the risk of

2 losing both foraging options by communicating before they had left the individual foraging

3 option.

4 Finally, in some of the tool transfer paradigms, chimpanzees handed tools over to

5 conspecifics predominantly upon "request" by the tool recipient (Yamamoto et al., 2009,

6 2012). Chimpanzees' requests consisted of extending their arms inside the compartment of

7 the other individual, clapping their hands, pounding against the panel between the

8 compartments, and vocalizations. When extending their arm inside the neighbor's

9 compartment to reach for the tool, chimpanzees' hands came very close to their partner due to

10 the small size of the compartments. This might be important with regard to the underlying

11 motivation here because chimpanzees could end these potentially harassing requests by

12 passing the tool over (cf. harassment avoidance explanations, see section 4.3.4 on food

13 sharing). In mother-offspring dyads, both participants showed requests at similar rates. In

14 non-kin dyads, predominantly dominant individuals produced requests toward subordinates,

15 which resulted in higher success rates for the dominants. Higher object transfer rates upon

16 request were also observed between chimpanzees in a token exchange paradigm (Yamamoto

17 and Tanaka, 2009) and between chimpanzees and capuchin monkeys, respectively, and

18 human experimenters (Barnes et al., 2008; Warneken et al., 2007). In another token-exchange

19 task that required apes to exchange tokens with each other before they could exchange the

20 token eventually with a human experimenter, orangutans but not chimpanzees, bonobos, or

21 gorillas frequently showed pointing and hand begging gestures toward their partner (Pelé et

22 al., 2009). One male orangutan (who showed the highest rates of pointing and begging) was

23 shown to receive more valuable tokens than expected by chance in response to pointing at

24 them but not after having begged for it by holding out his hand.

1   These findings from the cooperation literature are supported by experimental food sharing

2   studies in which typically a group of animals is provisioned with a large, high-value food

3   resource that can be monopolized by one individual. In six chimpanzee groups, begging

4   gestures usually preceded food transfers and producing begging gestures resulted in higher

5   transfer rates (Silk et al., 2013). Nevertheless, even when producing begging gestures

6   chimpanzees were successful in only 31% of cases. Begging gestures sometimes also

7   preceded food transfers in orangutans in a similar food sharing study conducted in a captive

8   group (Rossano and Liebal, 2014). However, this happened at lower rates than in the

9   chimpanzees studied by Silk and colleagues. On the other hand, begging in orangutans was

10   successful in 46% of cases. The same male orangutan who pointed at valuable tokens in the

11   study by Pelé and colleagues (2009) also offered food occasionally to females by moving

12   food toward them while looking at them (Rossano and Liebal, 2014).

13   *3.5   Summary*

14   While technical knowledge certainly can be used to solve problems with the participation of a

15   partner, there is evidence that individuals go beyond this. However, at this point some

16   important control conditions are still missing. For example, primates waiting for their partner

17   in the loose string paradigm might be explained simply in terms of sensitivity to the tension

18   of the string.

19   Direct interactions between individuals show high degrees of flexibility in how primates

20   manipulate each other. Great apes, in particular, show a wide range of manipulative

21   behaviors. Surprisingly, the normally semi-solitary orangutans appear to be very skilled at

22   exerting control over others in a highly flexibly manner. They manipulate others directly by

23   coercing them into executing certain actions, indirectly by providing access to resources, or

24   even by means of communication (e.g., pointing for a token). Chimpanzees have provided the

1   most examples of communication in cooperative contexts, such as attention-getters, begging

2   gestures, and solicitation. However, they are also the best-studied species. Therefore, it

3   remains unclear whether there are qualitative or quantitative differences between

4   chimpanzees and other nonhuman ape species in this respect.

5

6

7   **4.   From exploitation to helping: Motivational aspects of social interactions**

8   Aside from cognitive aspects, motivational aspects are critical for distinguishing between

9   various forms of social interactions. In most experimental studies, researchers assessed the

10   motivation of an individual by manipulating the food-related payoff structure of the task,

11   other costs such as physical efforts needed to help others, or the temporal extent of social

12   interactions (trial number, sequence, and duration). The types of interactions that we can

13   classify along a motivational axis (self – self+other – other-regarding) are exploitation,

14   mutualism, and helping (without or with costs for the helper).

15   We define exploitation as an act that benefits one individual at a cost for others (cf.

16   'manipulation' in Clutton-Brock, 2009). Exploitation typically occurs when the goals of two

17   individuals are in conflict. The motivation is usually self-regarding (or other-regarding

18   towards individuals other than the exploited individual).

19   Mutualism is defined as cooperation that results in direct benefits for each participant (e.g.,

20   Clutton-Brock, 2009). The benefits might be asymmetrically distributed or to some extent

21   delayed but, by definition, there must be a net gain for each participant. Mutualism is quite

22   mute with regard to underlying motives other than self-regarding ones.

1 Helping is defined as an act that benefits another individual but does not provide direct

2 benefits for the helper and might even entail costs for the helper (e.g., Warneken and

3 Tomasello, 2006). Usually helping is thought to be supported by prosocial motives. However,

4 there might also be instances of strategic helping in which helping is based on the expectation

5 of some kind of delayed gratification.

6 Punishment is defined as act that is detrimental to someone else, sometimes even at a cost for

7 the punisher. Punishment is not covered in detail in the current review. We mention it here

8 because it might be important for maintaining cooperation in the long run (in particular in the

9 case of third-party punishment). So far, however, there is little evidence for punishment

10 enforcing cooperation in nonhuman primates (e.g., Riedl et al., 2012). By definition,

11 punishment must not involve a direct benefit for the punisher and can be driven by antisocial

12 motives. However, it might also reflect an expectation of some kind of delayed gratification

13 (e.g., the punished individual might be more willing to cooperate in the future) or even

14 prosocial motives toward group members other than the punished individual (altruistic

15 punishment, e.g., Fehr and Gaechter, 2002).

16

17 *4.1   Self-regarding motivation*

18 Even in a cooperative problem-solving context, primates might pursue a self-regarding

19 optimal foraging strategy. Optimal foraging aims at maximizing own food intake while

20 keeping foraging costs at a minimum (e.g., Pyke et al., 1977). As cooperation can lead to

21 more efficient foraging, self-regarding motivation may be sufficient to account for mutualism

22 and social comparisons in the form of disadvantageous inequity aversion (i.e., aversive

23 responses when others receive more).

24   *4.1.1   Exploitation*

1   Even though there are many studies on food competition in nonhuman primates (cf. theory of

2   mind literature, for a recent review see Whiten, 2013), very few experimental studies have

3   examined how primates actively manipulate others to outcompete them. The theory of mind

4   literature focused on visual perspective taking and tracking others' knowledge and beliefs.

5   While these abilities might be beneficial for manipulating others, they do not necessarily

6   involve any direct social interaction.

7   Exploitative behaviors between individuals have been found in cooperation tasks with adult-

8   juvenile dyads in chimpanzees (Chalmeau, 1994), orangutans (Völter et al., 2015), and

9   Japanese macaques (Tokida et al., 1994). In these studies, adults physically manipulated

10   juveniles to access food for themselves. Other studies focused on tactical deception, which

11   involves using actions or communication outside their usual contexts and, thereby,

12   misleading others (Byrne and Whiten, 1988). However, most findings so far have concerned

13   primates inhibiting actions in the presence of competitors or hiding body parts from

14   competitors. In experimental studies, chimpanzees concealed their actions from competitors

15   (e.g., Karg et al., 2015; Melis et al., 2006a) but there is less experimental evidence that they

16   actively mislead others (in contrast to human children, e.g., Sodian et al., 1991). Two studies,

17   however, found that chimpanzees who had witnessed where a food reward was hidden

18   sometimes avoided this hiding place in the presence of a dominant conspecific (Hirata and

19   Matsuzawa, 2001; Menzel, 1974). Menzel (1974) reported that a juvenile chimpanzee

20   stopped uncovering food rewards in the presence of a dominant male who had stolen the food

21   from her before. In a few trials over an observation period of several months, she even moved

22   in the opposite direction from the food at first, thereby, leading the group away from the

23   food. Only when the dominant competitor was distracted by searching for the food

24   somewhere else she retrieved the food. Likewise, Hirata and Matsuzawa (2001) found

25   evidence for active misleading in one out of five chimpanzee dyads. After multiple days in

1 which a dominant competitor, who was ignorant of the food location, followed the subject to

2 the baited container, the subject started to approach the empty container first, thereby,

3 directing the attention of the competitor to the empty container. This behavior emerged for

4 the first time on day 24 of the experiment. Similar findings were obtained with mangabeys

5 (*Cercocebus torquatus torquatus*; Coussi-Korbel, 1994). Whether the chimpanzees and

6 mangabeys misled their competitors in the sense of producing a behavior to make others

7 belief that the food was elsewhere, however, remains contentious. Alternatively, the subjects

8 in these studies might have learned over multiple trials to avoid the baited container with the

9 competitor in their vicinity. Additionally, approaching the empty containers may have been

10 reinforced because it led the dominant individual to abandon the subject in order to search for

11 the food. These instances of primates leading competitors away from a food resource may

12 therefore constitute instances of learned deception not necessarily involving mental state

13 attribution.

14 *4.1.2   Mutualism*

15 In most cooperation studies, both partners receive a food reward when they solve the problem

16 together. Unless there is a choice between different alternatives (see prosocial choice task

17 below) or the pay-off is unbalanced (see advantageous inequity aversion, reciprocity, and

18 helping studies below), purely self-regarding motives may be sufficient to explain animals'

19 cooperative activities.

20 Mutualism has been shown in many primate species, including chimpanzees (e.g., Chalmeau,

21 1994; Crawford, 1937; Hirata and Fuwa, 2007; Melis et al., 2006b, c; Melis and Tomasello,

22 2013; Suchak et al., 2014), bonobos, *Pan paniscus* (Hare et al., 2007), orang-utans

23 (Chalmeau et al., 1997a; Völter et al., 2015), brown capuchin monkeys (Brosnan et al., 2006;

24 Chalmeau et al., 1997b; de Waal and Davis, 2003; Hattori et al., 2005; Visalberghi et al.,

2000), cottontop tamarins, *Saguinus oedipus* (Cronin et al., 2005; Cronin and Snowdon,

2008), and different macaque species, *Macaca tonkeana*, *M. mulatta*, *M. sylvanus* (Molesti

and Majolo, 2016; Petit et al., 1992).

Young chimpanzees engaged in cooperative activities with human caretakers; however,

mainly in a food acquisition context (Warneken et al., 2006). In contrast to children,

chimpanzees did not shows any sign of interest in social games with human caretakers that

did not involve food. Chimpanzees' cooperation is especially pronounced in mutualistic

settings (Greenberg et al., 2010). For example, when the food in the loose string paradigm is

clumped in the middle of the platform and, therefore, potentially monopolizable by one

individual, cooperation breaks down (Melis et al., 2006c). In general, when given the choice

chimpanzees as well as bonobos, orangutans, and marmosets (Bullinger et al., 2013;

Bullinger et al., 2011a; Rossano et al., in preparation; Rekers et al., 2011; but see Hare et al.,

2007) prefer to forage alone and thereby to maximize their own food intake. When a higher-

value food reward can be obtained by cooperating with others, chimpanzees and orangutans

flexibly switch to the cooperative alternative (Bullinger et al., 2011a; Rossano et al., in

preparation).

Cooperation in capuchin monkeys also declined when the food was clumped in the center of

the platform (de Waal and Davis, 2003). Other studies with distributed food rewards, which

slightly differed in value between the partners, found more tolerance towards unequal reward

distribution in capuchin monkeys (Brosnan et al., 2006). The latter finding might be

explained by the potentially high substitutability of the used rewards (Schwartz et al., 2016).

4.1.3 Disadvantageous inequity aversion

Disadvantageous inequity aversion describes negative reactions (e.g. refusals to accept or to

participate in a task) in response to witnessing someone else receiving more / better rewards

1   for the same labor. If appropriate controls confirm that the aversive response is not merely

2   driven by frustration induced by the loss of high-value food, inequity aversion can be framed

3   as a social comparison, one serving self-regarding motives, which might help to avoid being

4   outcompeted by group members.

5   The best studied primate species on inequity aversion is the brown capuchin monkey

6   (*Sapajus apella*). In a seminal study, female (but not male) capuchin monkeys refused food

7   rewards and stopped participating in a token exchange task when they observed how a

8   conspecific received higher value food rewards for engaging in the same activity (Brosnan

9   and de Waal, 2003). This effect was particularly pronounced when the subject had to work

10   harder (i.e. exchange more tokens) for a lower-value reward compared to the partner (van

11   Wolkenten et al., 2007, but see Fontenot et al., 2007). Extending these findings, in the

12   prosocial choice task, capuchins prefer a prosocial choice to a selfish one, but only if the

13   subject and its partner receive equal rewards (de Waal et al., 2008). When the partner had a

14   higher-value reward, subjects' choices did not deviate from chance, indicating that the

15   monkeys were less inclined to give their partner a better reward compared to themselves

16   (even when there were no costs for them). In a recent study, capuchin monkeys with no

17   access to a high-value food resource on a platform even punished conspecifics who had

18   access to the food by collapsing the food platform (Leimgruber et al., 2016). A no-partner

19   control condition ensured that the monkeys' behavior was aimed at the feeding conspecific

20   and not simply induced by frustration at inaccessible food. Capuchin monkeys punished at

21   equal rates in the presence of a feeding conspecific irrespective of whether the subject had

22   lost access to the food before or whether their partner had stolen the food from them. Fletcher

23   (2008) found additional evidence for disadvantageous inequity aversion. Here, male capuchin

24   monkeys were more likely to select the equal rewards option (rather than the unequal option)

25   when the partner was present but not when the partner was absent.

1   However, several studies could not replicate these findings with brown capuchin monkeys

2   (Fontenot et al., 2007; McAuliffe et al., 2015; Sheskin et al., 2014; Silberberg et al., 2009). It

3   has recently been suggested that differences in the value of food rewards and their

4   substitutability may explain the variable results across studies. Accordingly, differences in

5   value between high- and low-value food can be small despite clear differences in preference

6   tests (Schwartz et al 2016). Small differences in value between the food rewards, in turn, may

7   mask inequity-related responses.

8   Chimpanzees have also shown variable responses to disadvantageous inequity with some

9   studies providing positive evidence (Brosnan et al., 2005; Brosnan et al., 2010b) and others

10   showing no effect (Bräuer et al., 2009), or even an opposite effect when subjects received

11   unequal food without a task (Bräuer et al., 2006). Especially in a token exchange paradigm,

12   two chimpanzee samples refused to exchange tokens when they received lower value rewards

13   compared to conspecifics nearby (Brosnan et al., 2005; Brosnan et al., 2010b). Another group

14   of chimpanzees did not show such an effect using the same token-exchange paradigm and

15   controlling for order effects (Bräuer et al., 2009). Finally, a recent study found response to

16   inequity (i.e. refusals to participate in token exchanges) only in female chimpanzees but not

17   in males (Hopper et al., 2014).

18   Inequity aversion in chimpanzees has also been examined using a version of the mini-

19   ultimatum game in which one individual, the proposer, can propose an equal split of rewards

20   or an unequal split of rewards (favoring the proposer) to another individual, the responder.

21   The responder can then accept the proposed split for both individuals or it can reject the

22   rewards, which will result in neither getting any of the rewards. Chimpanzees (and bonobos)

23   accepted all non-zero offers by a conspecific, leading to the interpretation that they were

24   rationally maximizing their own payoffs without any evidence for social comparisons of the

25   reward distribution (Jensen et al., 2007; Kaiser et al., 2012; Proctor et al., 2013).

No evidence for disadvantageous inequity aversion was obtained for orangutans (Bräuer et al., 2006; Brosnan et al., 2011), bonobos (Bräuer et al., 2006; Kaiser et al., 2012), squirrel monkeys, *Saimiri sciureus* and *Saimiri boliviensis* (Freeman et al., 2013; Talbot et al., 2011), owl monkeys, *Aotus spp.* (Freeman et al., 2013), cotton top tamarins, *Saguinus oedipus* (Neiworth et al., 2009), or common marmosets, *Callithrix jacchus* (Freeman et al., 2013).

Recent studies have extended these findings by examining social evaluations based on third-party interactions. Brown capuchin monkeys observed an interaction between two humans in which one actor either helped the other one or not, or in which one actor reciprocated or failed to reciprocate a received favor (Anderson et al., 2013a; Anderson et al., 2013b). Subsequently, the actors simultaneously offered food to the monkeys. The results show that capuchin monkeys avoided humans that had been unhelpful or had failed to reciprocate in the previous interaction. Common marmosets and squirrel monkeys showed a similar bias in that they avoided non-reciprocators (Anderson et al., 2016; Kawai et al., 2014) though it has been argued that different mechanisms might underlie third-party evaluation in these two species than in capuchin monkeys (see Anderson et al., 2016). Similarly, chimpanzees preferred to beg for food from a human they had previously observed giving food to a human beggar (Russell et al., 2008). These findings suggest that certain primate species incorporate third-party interactions they have witnessed to evaluate foraging opportunities.

4.2   Self- & other-regarding motivation

Self- and other-regarding motives are certainly not mutually exclusive and they may carry the same or different weights when animals make decisions. As previously stated, mutualism *per se* does not provide evidence for other-regarding motivation. Sensitivity to others' pay-offs when there are no costs for the individual, as implemented in the prosocial choice task, may evidence prosocial motives (possibly besides self-regarding ones). That is, prosocial motives

1   can be identified when a subject prefers options that deliver more food to the partner while

2   the subject's pay-offs remain unchanged. Importantly, such a preference should not occur in

3   the absence of a partner (no-partner control condition). Furthermore, the impact of past

4   (short-term) interactions and (long-term) social relationships on primates' cooperative

5   behavior may be indicative of prosocial motives modulating their decisions.

6   *4.2.1   Prosocial choice task*

7   In the prosocial choice task, researchers try to minimize instrumental demands and the impact

8   of technical knowledge on the task performance. There are different versions of the task but

9   the basic comparison is between a selfish option yielding a benefit for the subject but not for

10   its partner (1/0 option), and a prosocial option resulting in a reward for the subject and its

11   partner (1/1 option). Crucially, choosing the prosocial option (compared to the selfish option)

12   does not involve costs for the subject. Prosocial choice tasks are operationalized either within

13   token-exchange paradigms or within bar- /string-pulling tasks. Each token and bar,

14   respectively, is associated with a certain payoff for the subject and the partner.

15   In the prosocial choice paradigm, unsolicited preferences for the prosocial option have been

16   found for capuchin monkeys (de Waal et al., 2008; Lakshminarayanan and Santos, 2008;

17   Suchak and de Waal, 2012; Takimoto and Fujita, 2011; Takimoto et al., 2010; but see Amici

18   et al., 2014), common marmosets (Burkart et al., 2007), and (dominant) long-tailed macaques

19   (Massen et al., 2010). In contrast, other species did not show consistent prosocial preferences,

20   such as Geoffroyi's spider monkeys (*Ateles geoffroyi*), bonobos, orangutans, and gorillas

21   (*Gorilla gorilla*; Amici et al., 2014b), and cotton-top tamarins (Cronin et al., 2009; Stevens,

22   2010). Most studies with chimpanzees did not find any evidence for prosocial preferences

23   (Amici et al., 2014b; Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008; Yamamoto and

24   Tanaka, 2010). In one study, however, female chimpanzees displayed a significant preference

for prosocial tokens over selfish ones irrespective of solicitation by the partner (Horner et al.,

2011). Unfortunately, token-exchange studies that provided evidence for prosocial choice so

far either did not include a control in which no partner was present (de Waal et al., 2008), or

this no-partner control condition was always administered after the social test condition

(Horner et al., 2011; Suchak and de Waal, 2012). Therefore, it remains ambiguous whether

chimpanzees' and capuchin monkeys' token preferences in the test compared to the control

condition result from an order effect.

In the bar-pulling paradigm, there is some evidence that capuchin monkeys prefer the

prosocial option specifically when the partner is present (compared to when it is not), but

only when the partner helped them to retrieve the food (Takimoto and Fujita, 2011). Other

bar-pulling studies found quite weak effects between the test condition and the no-partner

control condition (two-tailed p-value= 0.1; Lakshminarayanan and Santos, 2008) or found

that the effect depended on the dominance relationship between individuals (Takimoto et al.,

2010).

Additional factors that influenced prosocial choice in capuchin monkeys were the visibility

and familiarity of the partner and equal reward for both individuals (de Waal et al., 2008).

Interestingly, when the subjects could not see their partner anymore, their preference

switched from the prosocial option to the selfish one (de Waal et al., 2008; Takimoto et al.,

2010).

4.2.2   Short-term reciprocity

So far, we have looked at situations in which prosocial choices came with no costs for the

subject. Now, we turn to primate cooperation with unbalanced outcomes or even net losses

for the subject. Even if an individual is predominantly driven by self-regarding motives,

1   unbalanced or negative pay-offs may be tolerated. Mechanisms that allow for maintaining

2   cooperation in such cases can be (calculated) short-term reciprocity or reciprocity based on

3   long-term social relationships (see next section). In particular, turn-taking (or tit-for-tat)

4   strategies may constitute evidence for calculated short-term reciprocity.

5   Whether or not primates adopt turn-taking strategies has been examined using prosocial

6   choice tasks with alternating roles for the individuals. So far, these studies produced little

7   evidence for short-term reciprocity in nonhuman primates. Negative results have been

8   obtained for great apes including chimpanzees (Amici et al., 2014a; Melis et al., 2008; Pelé et

9   al., 2009; Yamamoto and Tanaka, 2009, 2010), bonobos, orangutans, and gorillas (Amici et

10   al., 2014a; Pelé et al., 2009), as well as monkey species such as Tonkean macaques (Pelé et

11   al., 2010), brown capuchin monkeys (Amici et al., 2014a; Pelé et al., 2010; Suchak and de

12   Waal, 2012), and spider monkeys (Amici et al., 2014a). There are few exceptions: one study

13   found some evidence for positive reciprocity in one out of 11 chimpanzee dyads (Brosnan et

14   al., 2009). Another study found evidence for calculated reciprocity in one non-kin orangutan

15   dyad (Dufour et al., 2009; Pelé et al., 2009). The two adult orangutans were reciprocally

16   exchanging tokens and food with each other. Over time, the exchanges became more

17   balanced between individuals and provided evidence for reciprocity within and between

18   trials. Moreover, cotton top tamarins' willingness to pull in a reward for the partner in a

19   prosocial choice task depended on whether or not the partner had pulled in rewards for the

20   subject before (Cronin et al. 2010).

21   Apart from the emergence of such turn-taking strategies, the question is whether primates

22   reciprocate received favors and select partners based on the outcome of recent interactions.

23   When chimpanzees in a cooperation or helping situation could choose between a conspecific

24   who had cooperated with them or helped them previously to obtain food and another one who

25   had not, chimpanzees did not prefer the former (Melis et al., 2008). Furthermore,

chimpanzees did not help more or share more in response to having cooperated with a conspecific partner previously (Greenberg et al., 2010; Hamann et al., 2011). In contrast, capuchin monkeys seem to take other's labor into consideration and distributed higher-value food to an individual who had helped them before (de Waal and Berger, 2000; Takimoto and Fujita, 2011).

In a recent instrumental helping study (Engelmann et al., 2015), chimpanzees could choose between a non-social option (low-value food for subject) and a social option (high-value food for partner). If they chose the social option, the partner could reciprocate the favor by pulling a string in return, which would result in a high-value reward for the subject. Chimpanzees were more likely to choose the risky option when a partner was present in the adjacent enclosure than when the partner was absent (no-partner control). Interestingly, when chimpanzees' willingness to reciprocate was experimentally manipulated, chimpanzees were more likely to take the risk when presented with a 'trustworthy' partner who always reciprocated compared to a 'non-trustworthy' partner who never reciprocated. This might suggest that chimpanzees are able to maintain reciprocal interactions if the partner is trustworthy. However, it is also possible that chimpanzees learned in the course of the ten trials per partner to adjust their behavior according to reinforcement schedule. Indeed, the likelihood of retrieving a reward and trustworthiness were identical in this study. In line with previous studies, the reciprocation rate in general was low (32% of trials in which the subjects chose the social option, see Engelmann et al., 2015, experiment 1) and not affected by the bonding status of the partners (Engelmann and Herrmann, 2016).

4.2.3 Factors affecting prosocial tendencies: kinship, dominance, tolerance, and trust

1   In this section, we address the impact of temporally more stable characteristics of social

2   relationships such as kinship, dominance hierarchies, tolerance, and bonding relationships on

3   primates' prosocial tendencies. Some of these factors are not independent. The precise

4   relation between these factors depends on the species and it is sometimes difficult to tease

5   their effects apart. For example, dominance relationships are often negatively correlated with

6   tolerance. Tolerance within dyads is in many species higher for kin compared to non-kin and

7   for bonding partners compared to other group members.

8   For chimpanzees (Suchak et al., 2014; Yamamoto and Tanaka, 2009) and capuchin monkeys

9   (Brosnan et al., 2006; de Waal and Davis, 2003) there is evidence that genetically related

10   dyads are more willing to help and cooperate with each other. Chimpanzee mother-offspring

11   dyads were more willing to help each other by transferring tools to each other (Yamamoto et

12   al., 2009). Moreover, chimpanzees were more likely to approach a cooperation problem-

13   solving apparatus when kin or unrelated individuals of similar rank were around (Suchak et

14   al., 2014). Similarly, capuchin monkey kin dyads were more tolerant toward clumped or

15   unequal food distribution in mutual cooperation tasks compared to non-kin dyads (Brosnan et

16   al., 2006; de Waal and Davis, 2003).

17   Dominance relations and tolerance play an important role as well. In the prosocial choice

18   tasks, higher-ranking individuals were more likely to choose the prosocial options for

19   subordinate individuals in capuchin monkeys (de Waal et al., 2008; Takimoto et al., 2010)

20   and long-tailed macaques (Massen et al., 2010). Dominance was also an important factor for

21   successful cooperation in common marmosets (*Callithrix jacchus*). In a helping task that

22   required one individual to pull a string so that the partner could grasp a bowl with food,

23   success varied widely between dyads (Werdenich and Huber, 2002). In successful dyads, the

24   subordinate individual would usually pull in the string and the dominant individual would

25   grasp the bowl with food. Subsequently, the dominant individual usually shared the spoils

1   with the subordinate. Thus, tolerance of subordinates by dominants was important for

2   cooperation in marmosets to occur.

3   In (non-kin) capuchin monkey dyads, in contrast, the dominant individual would monopolize

4   the food when the food was clumped on the platform in a cooperative bar-pulling task.

5   Consequently, subordinates stopped pulling in the platform with the clumped food (de Waal

6   and Davis, 2003). Similarly, in a cooperation task with unequal reward distribution, capuchin

7   monkey dyads in which the high-value reward was not consistently monopolized by one of

8   the individuals had much higher success rates (Brosnan et al., 2006). These findings suggest

9   that tolerance of dominant individuals toward subordinates is an important predictor of

10   successful cooperation.

11   In the loose string pulling paradigm, tolerance (i.e., co-feeding and food sharing rates) was

12   also an important predictor of success in chimpanzees (Melis et al., 2006c) and wild Barbary

13   macaques, *Macaca sylvanus* (Molesti and Majolo, 2016). In a recent study, chimpanzees

14   were more likely to choose a risky social option (success depended on the partner's

15   willingness to reciprocate) when paired with a close bonding partner compared to another

16   group member not closely bonded with the subject (Engelmann and Herrmann, 2016).

17   Differences in tolerance have been implicated in the fact that some species such as Tonkean

18   macaques (*Macaca tonkeana*) and bonobos are more successful in cooperative problem-

19   solving tasks than others like, for example, rhesus macaques (*Macaca mulatta*) and

20   chimpanzees (Hare et al., 2007; Petit et al., 1992; Tan and Hare, 2013). Similarly, common

21   marmosets have been found to be more willing to provide food for group members compared

22   to capuchin monkeys and Japanese macaques (Burkart and van Schaik, 2013). Success in the

23   'group service' task is in line with marmosets' higher co-feeding rates as compared to

24   capuchin monkeys and macaques.

25   *4.3   Other-regarding motivation*

1   Clear-cut cases of other-regarding motivation involve some costs for the helper (e.g. in terms

2   of losing foraging opportunities or of physical effort). Alternatively, other-regarding

3   motivation may be indicated when positive outcomes of a prosocial behavior cannot be

4   anticipated and reciprocation appears unlikely (Yamamoto and Takimoto, 2012). Indicators

5   of other-regarding motives might be instances of advantageous inequity aversion,

6   instrumental helping, and active food sharing.

7   *4.3.1   Advantageous inequity aversion*

8   Advantageous inequity aversion describes a situation in which an individual rejects better

9   pay-offs for him-/herself (compared to another individual) following equal labor of both

10   individuals. This type of inequity aversion is well established in humans even though it

11   varies across societies and has a later developmental onset than disadvantages inequity

12   aversion (e.g., Blake et al., 2015).

13   In contrast, for nonhuman primates, the evidence is sparse. For chimpanzees, there is only

14   one study suggesting that they reject high-value food rewards more often when their partner

15   receives a low-value food reward (inequity) compared to when the partner receives the same

16   high-value food (Brosnan et al., 2010b; but see Brosnan et al., 2005; Hopper et al., 2014).

17   Moreover, the behavior of proposers in the mini-ultimatum game has also been interpreted as

18   evidence for advantageous inequity aversion (Brosnan and de Waal, 2014). Such an

19   interpretation, however, is problematic because the key feature of the ultimatum game is that

20   the responder might reject any offer. Therefore, the proposer's choice might well be

21   influenced by the anticipated reaction of the responder. In fact, the only study that found a

22   preference for equal splits also found that chimpanzees preferred the selfish token when the

23   responder could not reject the offer (Proctor et al., 2013). Moreover, other studies that

24   implemented the ultimatum game with chimpanzees found no evidence that proposers would

25   favor equal splits (Jensen et al., 2007; Kaiser et al., 2012).

1   *4.3.2   Instrumental helping*

2   Instrumental helping tests include tasks in which the helper activates a mechanism or

3   transfers a resource to a recipient that will benefit the recipient but not the helper. Empty-

4   cage control tasks usually compare these helping situations to a baseline level in which no

5   one benefits from the activation of the mechanism or the resource transfer.

6   Initial evidence for instrumental helping in nonhuman primates has been obtained in tasks in

7   which a human experimenter was reaching for an out-of-reach object. Helping was assessed

8   by looking at whether nonhuman primates spontaneously transferred the object to the

9   experimenter. Chimpanzees picked up objects and passed them to humans at similar rates as

10   young human children (Warneken et al., 2007; Warneken and Tomasello, 2006). In

11   particular, young chimpanzees picked up objects more readily when their human caretaker

12   'accidentally' dropped the object and reached for it than when the caretaker intentionally

13   threw it on the floor (Warneken and Tomasello, 2006). In another study, juvenile and adult

14   chimpanzees passed an object to an unfamiliar human at equal rates irrespective of being

15   rewarded for it or whether there were some costs associated with helping (in the high cost

16   condition, chimpanzees had to climb up the mesh to retrieve the object). Importantly,

17   chimpanzees passed the object more often to the human when the latter was reaching for it

18   than not (Warneken et al., 2007).

19   In a similar setup, capuchin monkeys also helped human experimenters by picking up a target

20   object and passing it to the human who alternated her gaze between the object and the

21   monkey (Barnes et al., 2008). However, the monkeys were much more inclined to do so

22   when costs associated with helping were low (i.e. when the object was inside their enclosure

23   and they could easily transfer it to the human). Moreover, much like chimpanzees, capuchin

24   monkeys helped more often when the experimenter was actively reaching for the object.

25   Thus, reaching gestures seem to be an important cue for nonhuman primates and might

1   communicate the actor's goal to them, thereby, triggering their helping response. In some

2   sessions, capuchin monkeys and chimpanzees received a reward from the experimenter for

3   passing the object (Barnes et al., 2008; Warneken et al., 2007). Capuchin monkeys, in

4   contrast to chimpanzees, passed the object at higher rates when receiving a reward for it.

5   Even though monkeys could see whether or not a reward was in the hand of the experimenter

6   at the beginning of each trial, direct reinforcement for passing the tool in some trials poses a

7   problem for the interpretation of the motivational underpinnings of monkeys' helping

8   behavior. In general, studies involving human recipients are problematic regarding

9   motivational aspects of prosocial behavior given that the precise reinforcement history is

10   often unknown. Some authors note that captive primates regularly exchange objects with

11   humans (e.g., Barnes et al., 2008). Even in the absence of explicit training for passing objects

12   to human caretakers, animals might have been rewarded in the past for giving objects in their

13   enclosure back to their caretakers. Therefore, the motivation behind passing objects to

14   humans might reflect the expectation of receiving a reward at least occasionally in return.

15   Occasional reinforcement can lead to stable performance that is very robust to extinction (cf.

16   partial reinforcement effect; Amsel, 1962). Therefore, studies looking at interactions between

17   conspecifics may be more telling with regard to the underlying motivation.

18   In a very similar instrumental helping setting but with conspecific partners, chimpanzees

19   passed tools to group members located in adjacent cages (Yamamoto et al., 2009, 2012). Tool

20   transfers occurred more often in mother-offspring dyads compared to non-kin dyads.

21   Moreover, chimpanzees passed the tool mostly upon request from their partner (see previous

22   section on cognitive aspects). Tool transfer in mother-offspring dyads was selective and

23   sensitive to the needs of the partner in that they preferentially passed the tool that their

24   partner currently required (Yamamoto et al., 2012). One juvenile chimpanzee even actively

1   sought information about his mother's tool requirement (by standing up and looking through a

2   peephole between the adjacent compartments) before passing the correct tool to her.

3   Other studies showed that chimpanzees can release pegs to allow their non-kin partners to

4   enter a room with food or to activate a food (or token) delivering mechanism for a

5   conspecific (Melis et al., 2011; Warneken et al., 2007). Chimpanzees were more likely to

6   release the pegs if their partner was unsuccessfully trying to access the food. Moreover, in

7   one of these studies, distractors were used to reduce the baseline rate of "helping" even when

8   no partner was present (Melis et al 2011). This suggests that releasing the peg irrespective of

9   the partner's presence might be rewarding for apes.

10   Another study found quite high rates of instrumental helping in chimpanzees, which was in

11   most cases spontaneous and, in contrast to previous studies, not dependent on requests by the

12   individual that required help (Greenberg et al., 2010). In this study, chimpanzees were

13   presented with a modified version of the loose string paradigm in which two individuals had

14   to pull simultaneously to move a baited platform. The platform could be moved in two steps

15   in two sequential positions. In the helping condition, one chimpanzee (the helper) could

16   access her food after the first pull in the intermediate position of the platform whereas the

17   other chimpanzee could access her food only after the second pull when the board was in its

18   final position. Therefore, the latter chimpanzee was dependent upon the helper's willingness

19   to pull the rope one more time even when the helper had already received the food. Indeed,

20   chimpanzees helped their partner to obtain their piece food by pulling the platform one more

21   time.

22   However, it has recently been suggested that the results of Greenberg et al. (2010) might be

23   explained by the number of food items on the platform before the crucial second pulling step

24   (Albiach-Serrano, 2015). Even though chimpanzees were trained to pull the platform alone

25   by taking both ends of the rope and waiting for their partner, it was not established that they

1 knew when and where which piece of food was released in response to pulling the rope the

2 first and second time, respectively. The number of food pieces in the final position could, in

3 principle, explain the obtained pattern of results with the highest pulling rates in the

4 mutualistic condition (two pieces of food in the final position) followed by the helping

5 conditions (one piece of food in final position), and then the baseline condition (no food in

6 final position). A control condition to address this criticism would be to check whether

7 chimpanzees would also pull the platform to the final position even if their partner could not

8 access the food. Furthermore, pulling the platform to the end might have been rewarding for

9 chimpanzees because they could initiate the next trial in this way (if they did not pull the

10 platform to the final position, there was a delay of 60 or 30 seconds before the experimenter

11 started the next trial). At least for the first pairing of each subject, trials ended once both

12 individuals had received the food (or once the rope was inaccessible).

13 Similar to findings with chimpanzees (Yamamoto 2009), orangutans also passed tools

14 actively to their offspring even when they did not receive a reward throughout an entire

15 session (Völter et al., 2015). Adult orangutans continued passing the tools to adult group

16 members (kin and non-kin) even if they were not rewarded continuously (i.e., they were not

17 rewarded in 25% of trials, Rossano, Völter, and Call, in preparation).

18 Capuchin monkeys barely differentiated in an instrumental helping paradigm between a

19 partner being present or absent both when they were presented with food rewards and when

20 they received tokens that could be exchanged for food (Brosnan et al., 2010a). However, it is

21 possible that in some conditions a ceiling effect masked a difference between the social test

22 condition and the no-partner control condition. The only significant indication that their

23 partner's presence affected capuchin monkeys' performance was when there was no food for

24 the subject and a low-value reward for the partner. Here, the monkeys were more likely to

25 pull in the board when the partner was present. In contrast, when there was a high-value food

1 reward for the partner capuchin monkeys' performance did not deviate from the no-partner

2 control.

3   *4.3.3 Group service*

4 The group service task is a variant of the instrumental helping paradigm, which is

5 administered in group settings (thereby facilitating the application of the task to a large

6 number of species because it requires neither habituating individuals to being separated from

7 their group nor special testing facilities suitable for individual testing). In this task, one

8 individual needs to pull and hold a baited tray for other group members to access the food.

9 This individual is therefore paying a cost (i.e. no access to the food) for the benefit of others.

10 Common marmosets but not brown capuchin monkeys or Japanese macaques were found to

11 provide food for others consistently across multiple sessions (Burkart and van Schaik, 2013).

12 Marmosets pulled the tray without being solicited or harassed by others. Furthermore, a

13 control showed that marmosets hardly pulled the tray when the group members could not

14 access the food due to a fine grid that separated the monkeys and the food.

15 Using the same paradigm, a large-scale comparative study with 15 primate species provided

16 evidence for sustained prosocial pulling (at higher rates compared to a no-food control) in

17 four out of five common marmoset groups, white-faced sakis (*Pithecia pithecia*), cotton-top

18 tamarins, golden-headed lion tamarins (*Leontopithecus chrysomelas*), and siamangs

19 (*Hyblobates syndactylus*). No evidence for such sustained prosocial actions was found in

20 ring-tailed lemurs (*Lemur catta*), ruffed lemurs (*Varecia variegata*), spider monkeys, squirrel

21 monkeys (*Saimiri sciureus*), three groups of brown capuchin monkeys, Japanese and lion-

22 tailed macaques (*Macaca fuscata*, *M. silenus*), gibbons (*Hyblobates lar*), and chimpanzees

23 (Burkart et al., 2014). Interestingly, the best predictor of interspecies variance in prosociality

24 in this paradigm was the extent of allomaternal care typical of the species.

25   *4.3.4 Food sharing*

A detailed survey of primate food sharing studies is beyond the scope of the current article (for a recent review, see Jaeggi and Gurven, 2013a). Notwithstanding, we highlight here some findings relevant for the debate about other-regarding motives underpinning primate social interactions. Most instances of food sharing observed in nonhuman primates are passive or even enforced by the recipient despite resistance of the individual in possession of the food (Jaeggi and Gurven, 2013a). Instances of active, unsolicited food sharing are more informative about the presence of other-regarding motives. Active food sharing among unrelated adult individuals has been found, albeit at low rates, in chimpanzees (e.g., Silk et al., 2013), orangutans (Dufour et al., 2009; Rossano and Liebal, 2014), and brown capuchin monkeys (de Waal et al., 1993). Active food sharing between adult individuals and dependent offspring appears particularly pronounced in cooperatively breeding callitrichids (Brown et al., 2004) and is also present in great apes (e.g., Jaeggi et al., 2008; Silk, 1978). Harassment avoidance (Stevens, 2004) and reciprocity (Jaeggi and Gurven, 2013b) have been identified as predictors of food-sharing among non-kin individuals. Chimpanzees and squirrel monkeys, for example, were found to share more food when they were harassed by a conspecific (Stevens, 2004). Thus, even in the absence of other-regarding motives food sharing might arise to avoid costly harassment from others.

4.4 Summary

Overall, the results of prosocial choice, instrumental helping, group service, and food sharing tasks show a quite inconsistent pattern with many non-replications and high variance across studies that might result from different experimental paradigms (e.g., token exchange and bar pulling tasks), methodological differences within the same paradigm (e.g., the value of the food, proximity of the partners), and intraspecific variance between different groups (e.g., group composition and stability; see also Brosnan et al., 2010b). Therefore, it is too early to

draw any fixed conclusions about species differences with regard to social comparisons (in the form of inequity aversion) and prosocial motives. Future research should aim at clarifying the determinants that lead to the different study outcomes.

For chimpanzees and brown capuchin monkeys, as best-studied primate species in this context, prosocial tendencies were found mostly in situations in which there were no food-related costs for the subject. When helping or cooperation would potentially lead to competition over food between partners, helping or cooperation was rare. For capuchin monkeys, unbalanced payoffs may also hinder cooperation and helping. Chimpanzees seem to be more willing to pay a cost for others' welfare in terms of physical effort (e.g., climbing up a mesh to retrieve an object for someone else). Capuchin monkeys, in contrast, seem to be more willing to help when their own labor investment is small. In line with this, capuchin monkeys were also found to be more sensitive to others' labor and helped their partners more when the latter contributed to retrieve the reward.

Even in studies that found evidence for prosocial tendencies, the effects sizes are often rather small (e.g., Brosnan et al., 2010a; Burkart et al., 2007; Lakshminarayanan and Santos, 2008), which may explain the low replication rate. However, given a presumed publication bias for positive results, these findings should be interpreted with caution. Harassment avoidance might account for helping and food sharing in response to solicitation, requests, or noisy attempts to access the food (Stevens, 2004).

Finally, most studies so far have been somewhat biased toward prosocial behaviors, first, by not always giving subjects an alternative or opt-out option (e.g., instrumental helping tasks) and, second, by giving them a selfish and prosocial option but not a spiteful option (e.g., preventing others from accessing the food). More balanced experimental designs allowing animals to perform either in a prosocial, selfish, or spiteful manner towards conspecifics are needed. A good illustration of such an approach is a recent study, in which chimpanzees

1 could release a peg either to allow another individual to access food or to stop the individual

2 from accessing food. Chimpanzees were equally likely to release the peg in these two

3 conditions, suggesting that acts of instrumental helping might not necessarily be underpinned

4 by other-regarding motives (Tennie, Call, & Jensen. Submitted). These findings are in line

5 with a harassment avoidance account of helping behaviors in chimpanzees.

6 Finally, there is little evidence for calculated short-term reciprocity in nonhuman primates.

7 Long-term social relationships (including kinship, dominance relations, and friendships)

8 appear to be more relevant with regard to cooperation and helping. Social tolerance (usually

9 measured with co-feeding rates) seems to be the mediating variable between social

10 relationships and successful cooperation. The species-typical connection between social

11 relationships and tolerance might also explain species differences in how some social

12 variables (such as dominance) affect helping and cooperation.

13

14 **5. The relation between cognition and motivation: proximate and ultimate aspects**

15 Although coercion usually relates to self-regarding motives and sharing information (e.g.,

16 about the presence of a predator) is often linked to other-regarding motives, the two axes,

17 capturing motivational and cognitive aspects, are independent. For example, there are cases

18 in which acts of physical coercion may have prosocial motives. Mother rhesus macaques and

19 chacma baboons (*Papio ursinus*), for instance, have been observed to pull their infants back

20 to protect them from abuse by other individuals or other potentially dangerous situations

21 (Bolwig, 1959; Kawamura, 1959). However, similar actions may occur with quite different

22 underlying motives, for example, when male baboons try to avoid aggressive interactions by

23 picking up infants (cf. agonistic buffering, e.g. Strum, 1984). Social interactions not

24 involving physical coercion often depend on matching goals with both self- and, at least in

25 some instances, other-regarding motives at work. However, control over others can also be

1   indirect by granting access to relevant resources. Transfer of resources (such as tools or

2   tokens) between partners offers an example of such indirect control, which may serve self- or

3   other-regarding motives depending on the context.

4   Manipulative abilities and prosocial motivation may have quite different evolutionary origins.

5   Prosociality has been related to cooperative breeding (Burkart and van Schaik, 2016) whereas

6   social manipulation and deception have been related to living in complex social systems

7   (Byrne and Whiten, 1988; Dunbar, 1998). In a large test battery with 15 primate species,

8   allomaternal care was found to be the best predictor of prosocial behaviors in the group

9   service paradigm (Burkart et al., 2014). In line with this, the cooperative breeding hypothesis

10   suggests that cooperative breeders are more tolerant and prosocial and that these motivational

11   factors facilitate their performance in certain socio-cognitive tasks (Burkart and van Schaik,

12   2016).

13   While high tolerance may be a prerequisite for success in many cooperation problems and

14   social learning tasks, it does not predict more sophisticated socio-cognitive abilities *per se*.

15   Indeed, there is no evidence that cooperative breeders have advanced social manipulation,

16   communicative systems, or theory of mind abilities compared to other primates. Conversely,

17   species such as chimpanzees, macaques, and capuchin monkeys that performed rather poorly

18   in the group service paradigm (compared to cooperative breeders) provide the most

19   compelling evidence for highly flexible socio-cognitive abilities. Cooperation and

20   competition over resources in complex social systems has been hypothesized to be a driving

21   factor for the evolution of flexible socio-cognitive abilities (Byrne and Whiten, 1988;

22   Dunbar, 1998). These socio-cognitive abilities (such as visual perspective taking, goal

23   understanding, and social learning), in turn, may be advantageous for both social

24   manipulation and cooperation.

1   *5.1   Nonhuman primates compared to humans*

2   Already in young children, cooperation seems to be supported by an intrinsic prosocial

3   motivation and the relevant cognitive abilities scaffolding cooperation, such as understanding

4   others' communicative intentions, representing joint goals, and joint attention (Tomasello,

5   2010). Children prefer cooperating with others to working individually in a food acquisition

6   context (Rekers et al., 2011), and they share the spoils of their cooperation (Hamann et al.,

7   2011). Furthermore, communication allows children to coordinate their joint efforts

8   effectively (e.g., Duguid et al., 2014). They communicate not only to request help from others

9   and to achieve their own goals but also to help and inform them (e.g., Bullinger et al., 2011c;

10   Liszkowski et al., 2006).

11   In contrast, studies with nonhuman primates (in particular great apes) so far suggest either

12   that they prefer acquiring food individually to cooperating with others or that they are

13   indifferent (Bullinger et al., 2013; Bullinger et al., 2011a; Rekers et al., 2011). If they

14   communicate in cooperative situations at all (e.g., begging gestures in food sharing

15   situations), their communication seems to be driven by self-regarding motives to maximize

16   their own pay-off. Often communication in these situations serves to solicit help and support

17   from others (e.g., Duguid et al., 2014; Moore et al., 2015; Yamamoto et al., 2009).

18   Conversely, in an experimental context, there is no evidence for nonhuman primates

19   communicating to help others (e.g., Bullinger et al., 2014; with the exception of a field

20   experiment suggesting that chimpanzees warn unaware conspecifics when they encounter a

21   potentially dangerous situation, see Crockford et al., 2012). In line with that, chimpanzees,

22   reliably point to objects when they themselves can benefit from it but not to help humans

23   obtain a reward (Bullinger et al., 2011c). Chimpanzees' pointing gestures, therefore, have

24   been classified as imperative pointing (serving to request objects for themselves) but not as

declarative pointing to inform others (with the exception of language trained chimpanzees

who, according to some authors, produce declaratives, see Lyn et al., 2011; Rivas, 2005).

It has been proposed that the evolutionary origins of human cooperative communication can

be found in situations in which cooperation resulted in a mutually beneficial outcome

(Tomasello, 2010). In such situations, communication (based on shared intentions) may help

to coordinate cooperative activities, thereby, increasing the mutual pay-off. Nonhuman

primates' communication, however, differs from human communication significantly and can

be described as a form of social tool use mainly serving self-regarding goals. Warning calls

may be an exception to this characterization. For example, chimpanzees have been observed

to warn conspecifics when they encounter a potentially dangerous situation (Crockford et al.,

2012). It remains to be seen whether there are other cases of cooperative communication

outside the warning call system.

Manipulating others like a tool to fulfill self-regarding and in some cases other-regarding

motives appears fundamental for nonhuman primates' social interactions. Social tool use

shares some features with physical tool use, such as means-end reasoning and action

planning, but it differs from it in other aspects, such as the self-initiated actions by the social

tool. To what extent social tool use and cooperation are linked to physical tool use is

currently unclear. Interestingly, physical tool use and tactical deception rates in primates

(based on observational evidence) have both been correlated with the volume of executive

brain areas (Byrne and Corp, 2004; Reader and Laland, 2002). Moreover, so far the

experimental evidence for social tool use in nonhuman primates seems to be restricted to

tool-using species, such as chimpanzees, orangutans, and Japanese macaques (but there is

observational evidence for agonistic buffering in olive baboons, Barbary macaques, and

geladas). Therefore, cognitive processes supporting tool-use may well be related to social

manipulation. Shared variance between physical and social tool use might not only be found

1   at the species level but also within species at the individual level. Future research might

2   examine whether skilled tool-users show more elaborate forms of social manipulation

3   compared to tool-novices.

4   Social tool use usually involves self-initiated and self-controlled actions by the social tool. In

5   many situations, the social tool user must take such actions that are beyond its control into

6   account to achieve its goal. Due to the limited control over the social tool, sensitivity to the

7   goals and incentives of the social tool is important. In line with this, numerous studies in the

8   last two decades have shown that great apes (in particular, chimpanzees) and some monkey

9   species (e.g., rhesus macaques) are sensitive to the perception, knowledge states, and goals of

10   conspecific competitors (Whiten, 2013). The social tool-use account may allow us to bridge

11   the gap between theory of mind and cooperation. Future research should further explore the

12   relationship between manipulation and cooperation; first, by looking at cooperation (e.g.,

13   with in-group members) to compete with others (e.g., with out-group members) and, second,

14   by looking at social tool use and theory of mind abilities within cooperative situations (cf.

15   Schmelz and Call, 2016). The orangutan case study we presented illustrates how primates

16   manipulate one another while cooperating with each other. Importantly, manipulative

17   attempts do not exclude the existence of prosocial motives. Orangutans, for instance,

18   maintained cooperation across sessions in which there were no rewards for them.

19   The social tool use account may also explain why, according to the experimental literature,

20   chimpanzees and other primates conceal their actions from others but do not communicate to

21   mislead them (e.g., Karg et al., 2015; Melis et al., 2006a). Actively misleading other

22   individuals may – at least when it is flexible and not just a learned or innate strategy - not

23   only require to take others' perspectives and goals into account but may rely on the mutual

24   expectation that other individuals are helpful and truthful (Tomasello, 2010). Without such an

25   expectation, one should not assume that others follow misleading communicative signals.

This expectation may be a feature unique to humans. Understanding others in terms of their goals, and perception may be sufficient to account for cases of tactical deception and social tool use found in nonhuman primates (Whiten and Byrne, 1988)

6. Conclusions

In this paper, we classified a wide range of social interactions found in the experimental literature on nonhuman primates along a cognitive and a motivational axis. These axes work in conjunction to produce a variety of solutions to social problems (see Fig. 3).

With regard to the cognitive aspects, among nonhuman primates great apes seem to be particularly flexible in the ways they cooperate with one another and manipulate their partners. Chimpanzees and orangutans use different means to manipulate others, ranging from physical coercion to communication. Usually communication mainly serves to solicit help from others. Communication to help or inform others, in contrast, seems to be rare in nonhuman primates (with the notable exception of alarm calls, e.g., Seyfarth et al., 1980), unless they have received language training. Interestingly, despite their semi-solitary lifestyle, orangutans provide some of the most compelling evidence for flexible social manipulation involving physical coercion, indirect control by granting access to resources, and communication. Even though social behavior has been documented extensively in nonhuman primates, a broader phylogenetic assessment of social manipulation is missing in the experimental literature. Building on the rich observational evidence, more experimental work is required to elucidate the cognition behind social manipulation in primates, notably beyond the great ape clade.

1   With regard to motivational aspects, the last two decades have seen a growing number of

2   studies suggesting other-regarding preferences in nonhuman primates (that are not limited to

3   kin), in particular, in brown capuchin monkeys and chimpanzees. Long-term characteristics

4   of social relationships (including friendships, dominance, and kinship) appear to have a larger

5   impact on prosociality than short-term interactions, for instance in the form of calculated

6   reciprocity. However, the robustness of these findings is weakened by many non-replications.

7   Considerable inter-individual and inter-group variance seems to be a contributing factor for

8   the low replication rate together with methodological differences across studies. Identifying

9   the precise determinants of this high variance in results across studies will be a tedious but

10   critical endeavor in future research.

11   The most widely used paradigms in prosociality research are the prosocial choice task and

12   instrumental helping paradigms. On the one hand, prosocial choice tasks have the advantage

13   that animals have a clear choice between prosocial and selfish options. On the other hand,

14   instrumental helping studies usually include direct interactions between animals, which

15   makes them more interesting from a social manipulation point of view. Opt-out options or

16   spiteful alternatives should be implemented in these paradigms to assess whether the helping

17   behavior is really supported by other-regarding motives.

18   In general, many study designs in this area seem mainly aimed at showing prosocial but not

19   exploitative or even spiteful behaviors (for an exception, see Jensen et al., 2006). More

20   balanced paradigms are required that include exploitative options or that can elucidate

21   hierarchical structures of self- and other-regarding preferences. Prosocial choice tasks could

22   be extended for this purpose, for example, by introducing some costs for the subject (e.g., 2/0

23   vs 1/1). Comparing such a costly condition with the standard no-cost condition (1/0 vs 1/1)

24   might elucidate species-specific trade-offs between self- and other-regarding motivation.

25   Moreover, not all studies explicitly compared social and nonsocial situations (or the

conditions were not administered in a counterbalanced order). Without such no-partner control conditions, it remains unclear whether primates' prosocial behavior reflects other-regarding motives, a limited understanding of the task-relevant contingencies, or an intrinsic (self-regarding) preference for some particular options.

Finally, the social tool account of exploitation and cooperation in primates might be useful to close the gap between the theory of mind literature, which is mostly based on competitive situations and the work on prosocial motivation. Although some authors have argued that competitive contexts may have been the main setting for the evolution of mindreading abilities (e.g., Hare, 2001; Hare and Tomasello, 2004; Santos et al., 2006), cooperative contexts may have also played an important role. The reasons for underestimating the contribution of cooperative contexts are partly historical, with much more emphasis being placed on competition than cooperation in the area of comparative social cognition, and partly methodological, with competitive paradigms being easier to implement than cooperative ones (Schmelz and Call, 2016). Nevertheless, there is some evidence suggesting that individuals can take into account others' psychological states when communicating in non-competitive interactions (e.g., Crockford et al., 2012; Kaminski et al., 2004; Yamamoto et al., 2012). Comparing social manipulation and communication in competitive and cooperative situations will reveal how motivation and socio-cognitive abilities are related in different species. The experimental designs should also more often implement possibilities for (direct or indirect) partner control and partner choice (see Noë, 2006). This might also produce more evidence for manipulative and communicative strategies between partners. From a psychological perspective, manipulation and communication are particularly interesting when they are flexible and intentional. Therefore, it is important to examine whether primates use these behaviors in a context-specific manner, based on shared

1   experiences with certain individuals, while taking others' goals and incentives into

2   consideration.

3   Future research should aim at broadening the phylogenetic sample. In particular, species of

4   particular relevance with regard to their phylogenetic position or their socioecology should be

5   targeted while using standardized methods (as illustrated by recent studies, see Amici et al.,

6   2014a; Burkart et al., 2014). To achieve this, simple setups are required that do not require

7   extensive training or technical knowledge (see Albiach-Serrano 2015), especially to facilitate

8   comparisons with non-primates (Marshall-Pescini et al., 2016). Physiological measures of

9   emotional responsivity and arousal (such as pupil dilation, e.g., Hepach et al., 2012; and

10   thermal imaging, e.g., Kano et al., 2016) may allow to detect other-regarding preferences and

11   related cognitive biases (such as inequity aversion) even if they are not manifested

12   behaviorally. Future research on social interactions will benefit from using these measures

13   more widely as a complementary source of information to behavioral assessments.

14

1 Acknowledgements

4

5 Conflict of interest

7

8 Funding

1   References
2
3   Albiach-Serrano, A., 2015. Cooperation in primates: A critical, methodological review.

4   Interact. Stud. 16, 361-382.

5   Amici, F., Aureli, F., Call, J., 2008. Fission-fusion dynamics, behavioral flexibility, and

6   inhibitory control in primates. Curr. Biol. 18, 1415-1419.

7   Amici, F., Aureli, F., Mundry, R., Amaro, A.S., Barroso, A.M., Ferretti, J., Call, J., 2014a.

8   Calculated reciprocity? A comparative test with six primate species. Primates 55, 447-457.

9   Amici, F., Visalberghi, E., Call, J., 2014b. Lack of prosociality in great apes, capuchin

10   monkeys and spider monkeys: convergent evidence from two different food distribution

11   tasks. Proc. R. Soc. B 281, 20141699.

12   Amsel, A., 1962. Frustrative nonreward in partial reinforcement and discrimination learning:

13   some recent history and a theoretical extension. Psychol. Rev. 69, 306.

14   Anderson, J.R., Bucher, B., Kuroshima, H., Fujita, K., 2016. Evaluation of third-party

15   reciprocity by squirrel monkeys (*Saimiri sciureus*) and the question of mechanisms. Anim.

16   Cogn. 19, 813-818.

17   Anderson, J.R., Kuroshima, H., Takimoto, A., Fujita, K., 2013a. Third-party social evaluation

18   of humans by monkeys. Nat. Commun. 4, 1561.

19   Anderson, J.R., Takimoto, A., Kuroshima, H., Fujita, K., 2013b. Capuchin monkeys judge

20   third-party reciprocity. Cognition 127, 140-146.

21   Bard, K.A., 1990. "Social tool use" by free-ranging orangutans: A Piagetian and

22   developmental perspective on the manipulation of an animate object, in: Parker, S.T., Gibson,

23   K.R. (Eds.), 'Language' and intelligence in monkeys and apes: Comparative developmental

24   perspectives. Cambridge University Press, Cambridge, UK, pp. 356-378.

25   Barnes, J.L., Hill, T., Langer, M., Martinez, M., Santos, L.R., 2008. Helping behaviour and

26   regard for others in capuchin monkeys (*Cebus apella*). Biol. Lett. 4, 638-640.

Blake, P., McAuliffe, K., Corbit, J., Callaghan, T., Barry, O., Bowie, A., Kleutsch, L., Kramer, K., Ross, E., Vongsachang, H., 2015. The ontogeny of fairness in seven societies. Nature 528, 258–261.

Bolwig, N., 1959. A study of the behaviour of the chacma baboon, *Papio ursinus*. Behaviour 14, 136-162.

Bräuer, J., Call, J., Tomasello, M., 2006. Are apes really inequity averse? Proc. R. Soc. B 273, 3123-3128.

Bräuer, J., Call, J., Tomasello, M., 2009. Are apes inequity averse? New data on the token-exchange paradigm. Am. J. Primatol. 71, 175-181.

Brosnan, S., de Waal, F.B., 2003. Monkeys reject unequal pay. Nature 425, 297.

Brosnan, S.F., de Waal, F.B., 2014. Evolution of responses to (un)fairness. Science 346, 1251776.

Brosnan, S.F., Flemming, T., Talbot, C.F., Mayo, L., Stoinski, T., 2011. Orangutans (*Pongo pygmaeus*) do not form expectations based on their partner's outcomes. Folia Primatol. 82, 56-70.

Brosnan, S.F., Freeman, C., De Waal, F.B.M., 2006. Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. Am. J. Primatol. 68, 713-724.

Brosnan, S.F., Houser, D., Leimgruber, K., Xiao, E., Chen, T., de Waal, F.B., 2010a. Competing demands of prosociality and equity in monkeys. Evol. Hum. Behav. 31, 279-288.

Brosnan, S.F., Schiff, H.C., F.B.M., d.W., 2005. Tolerance for inequity may increase with social closeness in chimpanzees. Proc. R. Soc. B 272, 253-258.

Brosnan, S.F., Silk, J.B., Henrich, J., Mareno, M.C., Lambeth, S.P., Schapiro, S.J., 2009. Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. Anim. Cogn. 12, 587-597.

1   Brosnan, S.F., Talbot, C., Ahlgren, M., Lambeth, S.P., Schapiro, S.J., 2010b. Mechanisms

2   underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*. Anim.

3   Behav. 79, 1229-1237.

4   Brown, G.R., Almond, R.E., Bergen, Y.V., 2004. Begging, stealing, and offering: food

5   transfer in nonhuman primates. Adv. Stud. Behav. 34, 265-295.

6   Bullinger, A.F., Burkart, J.M., Melis, A.P., Tomasello, M., 2013. Bonobos, *Pan paniscus*,

7   chimpanzees, *Pan troglodytes*, and marmosets, *Callithrix jacchus*, prefer to feed alone. Anim.

8   Behav. 85, 51-60.

9   Bullinger, A.F., Melis, A.P., Tomasello, M., 2011a. Chimpanzees, *Pan troglodytes*, prefer

10   individual over collaborative strategies towards goals. Anim. Behav. 82, 1135-1141.

11   Bullinger, A.F., Melis, A.P., Tomasello, M., 2014. Chimpanzees (*Pan troglodytes*)

12   instrumentally help but do not communicate in a mutualistic cooperative task. J. Comp.

13   Psychol. 128, 251-260.

14   Bullinger, A.F., Wyman, E., Melis, A.P., Tomasello, M., 2011b. Coordination of

15   chimpanzees (*Pan troglodytes*) in a stag hunt game. Int. J. Primatol. 32, 1296-1310.

16   Bullinger, A.F., Zimmermann, F., Kaminski, J., Tomasello, M., 2011c. Different social

17   motives in the gestural communication of chimpanzees and human children. Dev. Sci. 14, 58-

18   68.

19   Burkart, J., van Schaik, C., 2016. Revisiting the consequences of cooperative breeding. J.

20   Zool. 299, 77.

21   Burkart, J.M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., Huber, J., Isler,

22   K., Kosonen, Z., Martins, E., 2014. The evolutionary origin of human hyper-cooperation.

23   Nat. Commun. 5.

1 Burkart, J.M., Fehr, E., Efferson, C., van Schaik, C.P., 2007. Other-regarding preferences in a

2 non-human primate: Common marmosets provision food altruistically. Proc. Natl. Acad. Sci.

3 U.S.A. 104, 19762-19766.

4 Burkart, J.M., van Schaik, C., 2013. Group service in macaques (*Macaca fuscata*), capuchins

5 (*Cebus apella*) and marmosets (*Callithrix jacchus*): a comparative approach to identifying

6 proactive prosocial motivations. J. Comp. Psychol. 127, 212-225.

7 Byrne, R.W., Corp, N., 2004. Neocortex Size Predicts Deception Rate in Primates. Proc. R.

8 Soc. B 271, 1693-1699.

9 Byrne, R.W., Whiten, A., 1988. Machiavellian intelligence: Social expertise and the

10 evolution of intellect in monkeys, apes and humans. Clarendon Press, Oxford, UK.

11 Chalmeau, R., 1994. Do chimpanzees cooperate in a learning task? Primates 35, 385-392.

12 Chalmeau, R., Gallo, A., 1993. Social constraints determine what is learned in the

13 chimpanzee. Behav. Process. 28, 173-179.

14 Chalmeau, R., Lardeux, K., Brandibas, P., Gallo, A., 1997a. Cooperative problem solving by

15 orangutans (*Pongo pygmaeus*). Int. J. Primatol. 18, 23-32.

16 Chalmeau, R., Visalberghi, E., Gallo, A., 1997b. Capuchin monkeys, *Cebus apella,* fail to

17 understand a cooperative task. Anim. Behav. 54, 1215-1225.

18 Chevalier-Skolnikoff, S., Liska, J., 1993. Tool use by wild and captive elephants. Anim.

19 Behav. 46, 209-219.

20 Clutton-Brock, T., 2009. Cooperation between non-kin in animal societies. Nature 462, 51-

21 57.

22 Coussi-Korbel, S., 1994. Learning to outwit a competitor in mangabeys (*Cercocebus*

23 *torquatus torquatus*). J. Comp. Psychol. 108, 164-171.

24 Crawford, M.P., 1937. The cooperative solving of problems by young chimpanzees. Comp.

25 Psychol. Monogr. 14, 1-88.

Crawford, M.P., 1941. The cooperative solving by chimpanzees of problems requiring serial responses to color cues. J. Soc. Psychol. 13, 259-280.

Crockford, C., Wittig, R.M., Mundry, R., Zuberbühler, K., 2012. Wild chimpanzees inform ignorant group members of danger. Curr. Biol. 22, 142-146.

Cronin, K.A., Kurian, A.V., Snowdon, C.T., 2005. Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). Anim. Behav. 69, 133-142.

Cronin, K.A., Schroeder, K.K., Rothwell, E.S., Silk, J.B., Snowdon, C.T., 2009. Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. J. Comp. Psychol. 123, 231-241.

Cronin, K.A., Snowdon, C.T., 2008. The effects of unequal reward distributions on cooperative problem solving by cottontop tamarins, *Saguinus oedipus*. Anim. Behav. 75, 245-257.

de Waal, F., Luttrell, L.M., Canfield, M.E., 1993. Preliminary data on voluntary food sharing in brown capuchin monkeys. Am. J. Primatol. 29, 73-78.

de Waal, F.B., Leimgruber, K., Greenberg, A.R., 2008. Giving is self-rewarding for monkeys. Proc. Natl. Acad. Sci. U.S.A. 105, 13685-13689.

de Waal, F.B.M., Berger, M.L., 2000. Payment for labour in monkeys. Nature 404, 563-563.

de Waal, F.B.M., Davis, J.M., 2003. Capuchin cognitive ecology: cooperation based on projected returns. Neuropsychologia 41, 221-228.

Deag, J.M., Crook, J.H., 1971. Social Behaviour and 'Agonistic Buffering' in the Wild Barbary Macaque *Macaca sylvana* L. Folia Primatol. 15, 183-200.

Dufour, V., Pelé, M., Neumann, M., Thierry, B., Call, J., 2009. Calculated reciprocity after all: computation behind token transfers in orang-utans. Biol. Lett. 5, 172-175.

Duguid, S., Wyman, E., Bullinger, A.F., Herfurth-Majstorovic, K., Tomasello, M., 2014. Coordination strategies of chimpanzees and human children in a Stag Hunt game. Proc. R. Soc. B 281, 20141973.

Dunbar, R.I., 1984. Infant-use by male gelada in agonistic contexts: agonistic buffering, progeny protection or soliciting support? Primates 25, 28-35.

Dunbar, R.I., 1998. The social brain hypothesis. Evol. Anthropol. 6, 178-190.

Engelmann, J.M., Herrmann, E., 2016. Chimpanzees Trust Their Friends. Curr. Biol. 26, 252-256.

Engelmann, J.M., Herrmann, E., Tomasello, M., 2015. Chimpanzees trust conspecifics to engage in low-cost reciprocity. Proc. R. Soc. B 282, 20142803.

Fehr, E., Gaechter, S., 2002. Altruistic punishment in humans. Nature 415.

Fletcher, G.E., 2008. Attending to the outcome of others: Disadvantageous inequity aversion in male capuchin monkeys (Cebus apella). Am. J. Primatol. 70, 901-905.

Fontenot, M., Watson, S., Roberts, K., Miller, R., 2007. Effects of food preferences on token exchange and behavioural responses to inequality in tufted capuchin monkeys, *Cebus apella*. Anim. Behav. 74, 487-496.

Freeman, H.D., Sullivan, J., Hopper, L.M., Talbot, C.F., Holmes, A.N., Schultz-Darken, N., Williams, L.E., Brosnan, S.F., 2013. Different responses to reward comparisons by three primate species. PLoS One 8, e76297.

Fujita, K., Kuroshima, H., Asai, S., 2003. How Do Tufted Capuchin Monkeys (*Cebus apella*) Understand Causality Involved in Tool Use? J. Exp. Psychol. Anim. Behav. Process. 29, 233-242.

Gómez, J.C., 1990. The emergence of intentional communication as a problem-solving strategy in gorilla, in: Parker, S.T., Gibson, K.R. (Eds.), 'Language' and intelligence in monkeys and apes. Cambridge University Press, Cambridge, UK, pp. 333-355.

Greenberg, J.R., Hamann, K., Warneken, F., Tomasello, M., 2010. Chimpanzee helping in collaborative and noncollaborative contexts. Anim. Behav. 80, 873-880.

Hamann, K., Warneken, F., Greenberg, J.R., Tomasello, M., 2011. Collaboration encourages equal sharing in children but not in chimpanzees. Nature 476, 328-331.

Hare, B., 2001. Can competitive paradigms increase the validity of experiments on primate social cognition? Anim. Cogn. 4, 269-280.

Hare, B., Melis, A.P., Woods, V., Hastings, S., Wrangham, R., 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. Curr. Biol. 17, 619-623.

Hare, B., Tomasello, M., 2004. Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. Anim. Behav. 68, 571-581.

Hattori, Y., Kuroshima, H., Fujita, K., 2005. Cooperative problem solving by tufted capuchin monkeys (*Cebus apella*): Spontaneous division of labor, communication, and reciprocal altruism. J. Comp. Psychol. 119, 335-342.

Hepach, R., Vaish, A., Tomasello, M., 2012. Young children are intrinsically motivated to see others helped. Psychol. Sci. 23, 967-972.

Herrmann, E., Wobber, V., Call, J., 2008. Great apes'(*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. J. Comp. Psychol. 122, 220-230.

Heyes, C., 2015. Animal mindreading: what's the problem? Psychon Bull Rev 22, 313-327.

Hirata, S., Fuwa, K., 2007. Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. Primates 48, 13-21.

Hirata, S., Matsuzawa, T., 2001. Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). Anim. Cogn. 4, 285-295.

Hopper, L.M., Lambeth, S.P., Schapiro, S.J., Brosnan, S.F., 2014. Social comparison mediates chimpanzees' responses to loss, not frustration. Anim. Cogn. 17, 1303-1311.

Horner, V., Carter, J.D., Suchak, M., de Waal, F.B., 2011. Spontaneous prosocial choice by chimpanzees. Proc. Natl. Acad. Sci. U.S.A. 108, 13847-13851.

Jaeggi, A.V., Gurven, M., 2013a. Natural cooperators: food sharing in humans and other primates. Evol. Anthropol. 22, 186-195.

Jaeggi, A.V., Gurven, M., 2013b. Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. Proc. R. Soc. B 280, 20131615.

Jaeggi, A.V., Van Noordwijk, M.A., Van Schaik, C.P., 2008. Begging for information: mother–offspring food sharing among wild Bornean orangutans. Am. J. Primatol. 70, 533-541.

Jensen, K., Call, J., Tomasello, M., 2007. Chimpanzees are rational maximizers in an ultimatum game. Science 318, 107-109.

Jensen, K., Hare, B., Call, J., Tomasello, M., 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. Proc. R. Soc. B 273, 1013-1021.

Kaiser, I., Jensen, K., Call, J., Tomasello, M., 2012. Theft in an ultimatum game: chimpanzees and bonobos are insensitive to unfairness. Biol. Lett. 8, 942–945.

Kaminski, J., Call, J., Tomasello, M., 2004. Body orientation and face orientation: two factors controlling apes' begging behavior from humans. Anim. Cogn. 7, 216-223.

Kano, F., Hirata, S., Deschner, T., Behringer, V., Call, J., 2016. Nasal temperature drop in response to a playback of conspecific fights in chimpanzees: A thermo-imaging study. Physiol. Behav. 155, 83-94.

Karg, K., Schmelz, M., Call, J., Tomasello, M., 2015. Chimpanzees strategically manipulate what others can see. Anim. Cogn. 18, 1069-1076.

Kawai, N., Yasue, M., Banno, T., Ichinohe, N., 2014. Marmoset monkeys evaluate third-party reciprocity. Biol. Lett. 10, 20140058.

Kawamura, S., 1959. The process of sub-culture propagation among Japanese macaques. Primates 2, 43-60.

Köhler, W., 1925. The mentality of apes. Routledge and Kegan Paul, London, UK.

Lakshminarayanan, V.R., Santos, L.R., 2008. Capuchin monkeys are sensitive to others' welfare. Curr. Biol. 18, R999-R1000.

Lefebvre, L., Reader, S.M., Sol, D., 2004. Brains, innovations and evolution in birds and primates. Brain Behav. Evol. 63, 233-246.

Leimgruber, K.L., Rosati, A.G., Santos, L.R., 2016. Capuchin monkeys punish those who have more. Evol. Hum. Behav. 37, 236-244.

Liszkowski, U., Carpenter, M., Striano, T., Tomasello, M., 2006. 12-and 18-month-olds point to provide information for others. J. Cog. Dev. 7, 173-187.

Lyn, H., Greenfield, P.M., Savage-Rumbaugh, S., Gillespie-Lynch, K., Hopkins, W.D., 2011. Nonhuman primates do declare! A comparison of declarative symbol and gesture use in two children, two bonobos, and a chimpanzee. Lang. Commun. 31, 63-74.

MacLean, E.L., Merritt, D.J., Brannon, E.M., 2008. Social complexity predicts transitive reasoning in prosimian primates. Anim. Behav. 76, 479-486.

Manrique, H.M., Gross, A.N.M., Call, J., 2010. Great apes select tools on the basis of their rigidity. J. Exp. Psychol. Anim. Behav. Process. 36, 409-422.

Manrique, H.M., Sabbatini, G., Call, J., Visalberghi, E., 2011. Tool choice on the basis of rigidity in capuchin monkeys. Anim. Cogn. 14, 775-786.

Marshall-Pescini, S., Dale, R., Quervel-Chaumette, M., Range, F., 2016. Critical issues in experimental studies of prosociality in non-human species. Anim. Cogn. 19, 679-705.

Massen, J.J., Ritter, C., Bugnyar, T., 2015. Tolerance and reward equity predict cooperation in ravens (*Corvus corax*). Sci. Rep. 5, 15021.

Massen, J.J., Van Den Berg, L.M., Spruijt, B.M., Sterck, E.H., 2010. Generous leaders and selfish underdogs: pro-sociality in despotic macaques. PLoS One 5, e9734.

McAuliffe, K., Chang, L.W., Leimgruber, K.L., Spaulding, R., Blake, P.R., Santos, L.R., 2015. Capuchin monkeys, *Cebus apella*, show no evidence for inequity aversion in a costly choice task. Anim. Behav. 103, 65-74.

Melis, A.P., Call, J., Tomasello, M., 2006a. Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. J. Comp. Psychol. 120, 154-162.

Melis, A.P., Hare, B., Tomasello, M., 2006b. Chimpanzees recruit the best collaborators. Science 311, 1297-1300.

Melis, A.P., Hare, B., Tomasello, M., 2006c. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. Anim. Behav. 72, 275-286.

Melis, A.P., Hare, B., Tomasello, M., 2008. Do chimpanzees reciprocate received favours? Anim. Behav. 76, 951-962.

Melis, A.P., Tomasello, M., 2013. Chimpanzees' (*Pan troglodytes*) strategic helping in a collaborative task. Biol. Lett. 9, 20130009.

Melis, A.P., Warneken, F., Jensen, K., Schneider, A.-C., Call, J., Tomasello, M., 2011. Chimpanzees help conspecifics obtain food and non-food items. Proc. R. Soc. B 278, 1405-1413.

Menzel, E., 1974. A group of young chimpanzees in a one-acre field., in: Schrier, A., Stollnitz, F. (Eds.), Behavior of Nonhuman Primates. Academic Press, New York, pp. 83-153.

Molesti, S., Majolo, B., 2016. Cooperation in wild Barbary macaques: factors affecting free partner choice. Anim. Cogn. 19, 133-146.

1   Moore, R., Call, J., Tomasello, M., 2015. Production and comprehension of gestures between

2   orang-utans (*Pongo pygmaeus*) in a referential communication game. PLoS One 10,

3   e0129726.

4   Mulcahy, N., Call, J., Dunbar, R.I.M., 2005. Gorillas (*Gorilla gorilla*) and orangutans (*Pongo*

5   *pygmaeus*) encode relevant problem features in a tool-using task. J. Comp. Psychol. 119, 23–

6   32.

7   Neiworth, J.J., Johnson, E.T., Whillock, K., Greenberg, J., Brown, V., 2009. Is a sense of

8   inequity an ancestral primate trait? Testing social inequity in cotton top tamarins (*Saguinus*

9   *oedipus*). J. Comp. Psychol. 123, 10-17.

10   Noë, R., 2006. Cooperation experiments: coordination through communication versus acting

11   apart together. Anim. Behav. 71, 1-18.

12   Ostojić, L., Clayton, N.S., 2014. Behavioural coordination of dogs in a cooperative problem-

13   solving task with a conspecific and a human partner. Anim. Cogn. 17, 445-459.

14   Pelé, M., Dufour, V., Thierry, B., Call, J., 2009. Token transfers among great apes (*Gorilla*

15   *gorilla*, *Pongo pygmaeus*, *Pan paniscus*, and *Pan troglodytes*): species differences, gestural

16   requests, and reciprocal exchange. J. Comp. Psychol. 123, 375-384.

17   Pelé, M., Thierry, B., Call, J., Dufour, V., 2010. Monkeys fail to reciprocate in an exchange

18   task. Anim. Cogn. 13, 745-751.

19   Péron, F., Rat-Fischer, L., Lalot, M., Nagle, L., Bovet, D., 2011. Cooperative problem

20   solving in African grey parrots (*Psittacus erithacus*). Anim. Cogn. 14, 545-553.

21   Petit, O., Desportes, C., Thierry, B., 1992. Differential probability of "coproduction" in two

22   species of macaque (*Macaca tonkeana*, *M. mulatta*). Ethology 90, 107-120.

23   Plotnik, J.M., Lair, R., Suphachoksahakun, W., de Waal, F.B., 2011. Elephants know when

24   they need a helping trunk in a cooperative task. Proc. Natl. Acad. Sci. U.S.A. 108, 5116-

25   5121.

Povinelli, D.J., 2000. Folk physics for apes: the chimpanzee's theory of how the world works. Oxford University Press, New York, NY.

Povinelli, D.J., O'Neill, D.K., 2000. Do chimpanzees use their gestures to instruct each other, in: Baron-Cohen, S., Tager-Flusberg, H., Cohen, D.J. (Eds.), Understanding other minds: Perspectives from developmental cognitive neuroscience. Oxford University Press, New York, NY.

Proctor, D., Williamson, R.A., de Waal, F.B., Brosnan, S.F., 2013. Chimpanzees play the ultimatum game. Proc. Natl. Acad. Sci. U.S.A. 110, 2070-2075.

Pusey, A.E., 1983. Mother-offspring relationships in chimpanzees after weaning. Anim. Behav. 31, 363-377.

Pyke, G.H., Pulliam, H.R., Charnov, E.L., 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52, 137-154.

Reader, S.M., Laland, K.N., 2002. Social intelligence, innovation, and enhanced brain size. Proc. Natl. Acad. Sci. U.S.A. 99, 4436-4441.

Rekers, Y., Haun, D., Tomasello, M., 2011. Children, but not chimpanzees, prefer to collaborate. Curr. Biol. 21, 1756-1758.

Riedl, K., Jensen, K., Call, J., Tomasello, M., 2012. No third-party punishment in chimpanzees. Proc. Natl. Acad. Sci. U.S.A. 109, 14824-14829.

Rivas, E., 2005. Recent use of signs by chimpanzees (*Pan troglodytes*) in interactions with humans. J. Comp. Psychol. 119, 404-417.

Rossano, F., Liebal, K., 2014. "Requests" and "offers" in orangutans and human infants, in: Drew, P., Couper-Kuhlen, E. (Eds.), Requesting in Social Interaction. John Benjamins Publishing Company, Amsterdam, The Netherlands, pp. 335-363.

Russell, Y.I., Call, J., Dunbar, R.I., 2008. Image scoring in great apes. Behav. Process. 78, 108-111.

Santos, L.R., Flombaum, J.I., Phillips, W., 2006. The evolution of human mindreading: How non-human primates can inform social cognitive neuroscience, in: Platek, S., Keenan, J.P., Shackelford, T.K. (Eds.), Evolutionary Cognitive Neuroscience. MIT Press, Cambridge, pp. 433-456.

Savage-Rumbaugh, E.S., Rumbaugh, D.M., Boysen, S., 1978. Symbolic communication between two chimpanzees (*Pan troglodytes*). Science 201, 641-644.

Schmelz, M., Call, J., 2016. The psychology of primate cooperation and competition: a call for realigning research agendas. Phil. Trans. R. Soc. B 371, 20150067.

Schrauf, C., Call, J., 2011. Great apes use weight as a cue to find hidden food. Am. J. Primatol. 73, 323-334.

Schrauf, C., Call, J., Fuwa, K., Hirata, S., Santos, L., 2012. Do chimpanzees use weight to select hammer tools. PLoS One 7, e41044-e41044.

Schwartz, L.P., Silberberg, A., Casey, A.H., Paukner, A., Suomi, S.J., 2016. Scaling reward value with demand curves versus preference tests. Anim. Cogn., 1-11.

Seed, A., Mayer, C., in press. Problem-solving in animals in: Call, J. (Ed.), APA Handbook of Comparative Psychology. American Psychological Association.

Seed, A.M., Clayton, N.S., Emery, N.J., 2008. Cooperative problem solving in rooks (*Corvus frugilegus*). Proc. R. Soc. B 275, 1421-1429.

Seyfarth, R.M., Cheney, D.L., Marler, P., 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. Anim. Behav. 28, 1070-1094.

Sheskin, M., Ashayeri, K., Skerry, A., Santos, L.R., 2014. Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation. Evol. Hum. Behav. 35, 80-88.

Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J.R., Visalberghi, E., 2009. Does inequity aversion depend on a frustration effect? A test with capuchin monkeys (*Cebus apella*). Anim. Cogn. 12, 505-509.

Silk, J.B., 1978. Patterns of food sharing among mother and infant chimpanzees at Gombe National Park, Tanzania. Folia Primatol. 29, 129-141.

Silk, J.B., Brosnan, S.F., Henrich, J., Lambeth, S.P., Shapiro, S., 2013. Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. Anim. Behav. 85, 941-947.

Silk, J.B., Brosnan, S.F., Vonk, J., Henrich, J., Povinelli, D.J., Richardson, A.S., Lambeth, S.P., Mascaro, J., Schapiro, S.J., 2005. Chimpanzees are indifferent to the welfare of unrelated group members. Nature 437, 1357-1359.

Sodian, B., Taylor, C., Harris, P.L., Perner, J., 1991. Early deception and the child's theory of mind: False trails and genuine markers. Child Dev. 62, 468-483.

Stephens, D.W., McLinn, C.M., Stevens, J.R., 2002. Discounting and reciprocity in an iterated prisoner's dilemma. Science 298, 2216-2218.

Stevens, J.R., 2004. The selfish nature of generosity: harassment and food sharing in primates. Proc. R. Soc. B 271, 451-456.

Stevens, J.R., 2010. Donor payoffs and other-regarding preferences in cotton-top tamarins (*Saguinus oedipus*). Anim. Cogn. 13, 663-670.

Strum, S.C., 1983. Use of females by male olive baboons (*Papio anubis*). Am. J. Primatol. 5, 93-109.

Strum, S.C., 1984. Why males use infants, in: Taub, D.M. (Ed.), Primate Paternalism. Van Nostrand Reinhold Company, New York, NY.

Suchak, M., de Waal, F.B., 2012. Monkeys benefit from reciprocity without the cognitive burden. Proc. Natl. Acad. Sci. U.S.A. 109, 15191-15196.

Suchak, M., Eppley, T.M., Campbell, M.W., de Waal, F.B., 2014. Ape duos and trios: spontaneous cooperation with free partner choice in chimpanzees. PeerJ 2, e417.

Takimoto, A., Fujita, K., 2011. I acknowledge your help: Capuchin monkeys' sensitivity to others' labor. Anim. Cogn. 14, 715-725.

Takimoto, A., Kuroshima, H., Fujita, K., 2010. Capuchin monkeys (*Cebus apella*) are sensitive to others' reward: an experimental analysis of food-choice for conspecifics. Anim. Cogn. 13, 249-261.

Talbot, C.F., Freeman, H.D., Williams, L.E., Brosnan, S.F., 2011. Squirrel monkeys' response to inequitable outcomes indicates a behavioural convergence within the primates. Biol. Lett. 7, 680-682.

Tan, J., Hare, B., 2013. Bonobos share with strangers. PLoS One 8, e51922.

Tebbich, S., Taborsky, M., Winkler, H., 1996. Social manipulation causes cooperation in keas. Anim. Behav. 52, 1-10.

Tokida, E., Tanaka, I., Takefushi, H., Hagiwara, T., 1994. Tool-using in Japanese macaques: use of stones to obtain fruit from a pipe. Anim. Behav. 47, 1023-1030.

Tomasello, M., 2010. Origins of human communication. The MIT press, Cambridge, MA.

van Noordwijk, M.A., van Schaik, C.P., 2005. Development of ecological competence in Sumatran orangutans. Am J Phys Anthropol 127, 79-94.

van Wolkenten, M., Brosnan, S.F., de Waal, F.B., 2007. Inequity responses of monkeys modified by effort. Proc. Natl. Acad. Sci. U.S.A. 104, 18854-18859.

Visalberghi, E., Quarantotti, B.P., Tranchida, F., 2000. Solving a cooperation task without taking into account the partner's behavior: The case of capuchin monkeys (*Cebus apella*). J. Comp. Psychol. 114, 297.

Völter, C.J., Call, J., in press. Causal and Inferential Reasoning in Animals, in: Call, J. (Ed.), APA Handbook of Comparative Psychology. American Psychological Association.

Völter, C.J., Rossano, F., Call, J., 2015. From exploitation to cooperation: social tool use in orang-utan mother–offspring dyads. Anim. Behav. 100, 126-134.

Vonk, J., Brosnan, S.F., Silk, J.B., Henrich, J., Richardson, A.S., Lambeth, S.P., Schapiro, S.J., Povinelli, D.J., 2008. Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. Anim. Behav. 75, 1757-1770.

Warneken, F., Chen, F., Tomasello, M., 2006. Cooperative activities in young children and chimpanzees. Child Dev. 77, 640-663.

Warneken, F., Hare, B., Melis, A.P., Hanus, D., Tomasello, M., 2007. Spontaneous altruism by chimpanzees and young children. PLoS Biol. 5, e184.

Warneken, F., Tomasello, M., 2006. Altruistic helping in human infants and young chimpanzees. Science 311, 1301-1303.

Werdenich, D., Huber, L., 2002. Social factors determine cooperation in marmosets. Anim. Behav. 64, 771-781.

Whiten, A., 2013. Humans are not alone in computing how others see the world. Anim. Behav. 86, 213-221.

Whiten, A., Byrne, R.W., 1988. Tactical deception in primates. Behav. Brain. Sci. 11, 233-244.

Whiten, A., Rumsey, T.J., 1973. 'Agonistic buffering'in the wild barbary macaque, *Macaca sylvana* L. Primates 14, 421-425.

Yamamoto, S., Humle, T., Tanaka, M., 2009. Chimpanzees help each other upon request. PLoS One 4, e7416.

Yamamoto, S., Humle, T., Tanaka, M., 2012. Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. Proc. Natl. Acad. Sci. U.S.A. 109, 3588-3592.

Yamamoto, S., Takimoto, A., 2012. Empathy and fairness: Psychological mechanisms for eliciting and maintaining prosociality and cooperation in primates. Soc. Justice Res. 25, 233-255.

1 Yamamoto, S., Tanaka, M., 2009. Do chimpanzees (*Pan troglodytes*) spontaneously take

2 turns in a reciprocal cooperation task? J. Comp. Psychol. 123, 242-249.

3 Yamamoto, S., Tanaka, M., 2010. The influence of kin relationship and reciprocal context on

4 chimpanzees' other-regarding preferences. Anim. Behav. 79, 595-602.

5

6

1   Figure captions

2   Figure 1. Social interactions can be classified along (a) a cognitive axis and (b) a motivational

3   axis. Both axes focus on the proximate mechanisms underlying social interactions.

4   Figure 2. Examples of social tool use and cooperation in orangutans (*Pongo abelii*). *a* and *b.*

5   Orangutan mothers coerced their offspring into retrieving a food reward by guiding their

6   arms and bodies toward a food reward and pulling them back as soon as the juveniles grabbed

7   the food. *c*. If necessary to obtain a food reward, orangutans spontaneously passed a tool to

8   their offspring. The offspring could use the tool to activate a mechanism that eventually

9   would deliver food to both of them. *d*. Adult orangutans cooperated by passing a tool to each

10   other. When the tool recipient had a nonsocial alternative apparatus mounted below the

11   cooperation apparatus, orangutans started to pass the tool high above their head, presumably

12   to influence their partner's decision in favor of the cooperative option.

13   Figure 3. In conjunction, the cognitive and motivational axes capture a wide range of primate
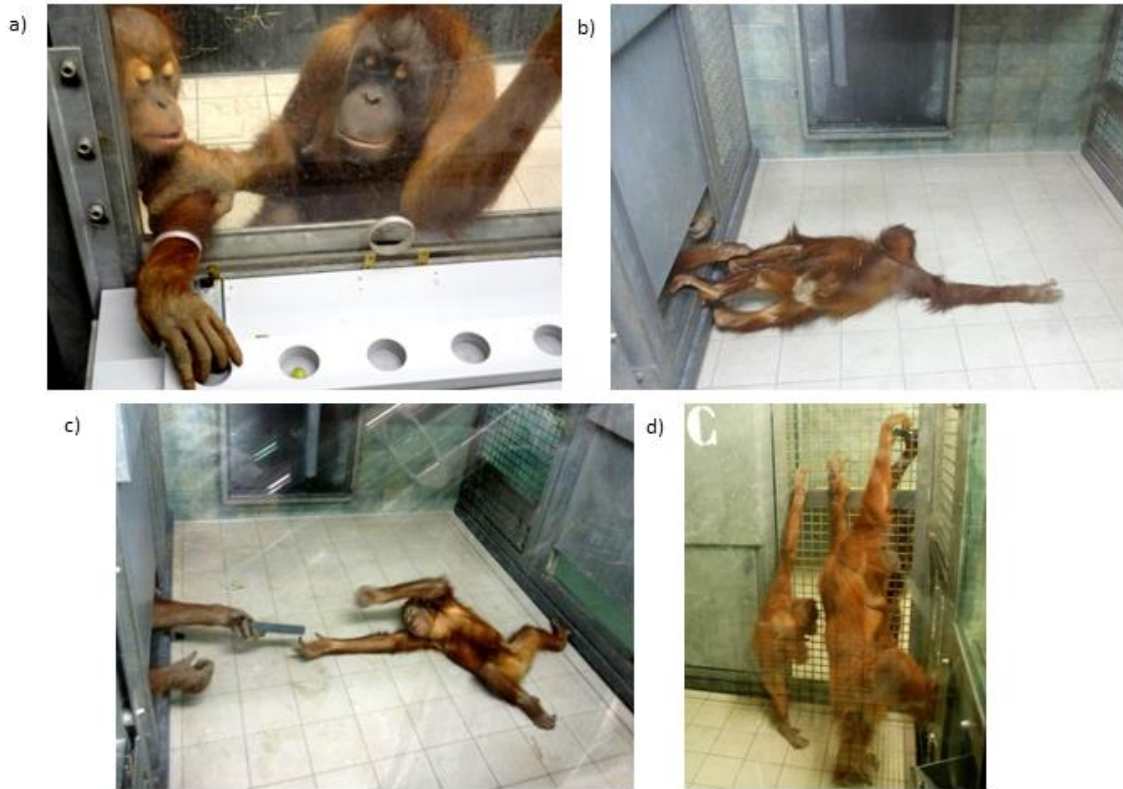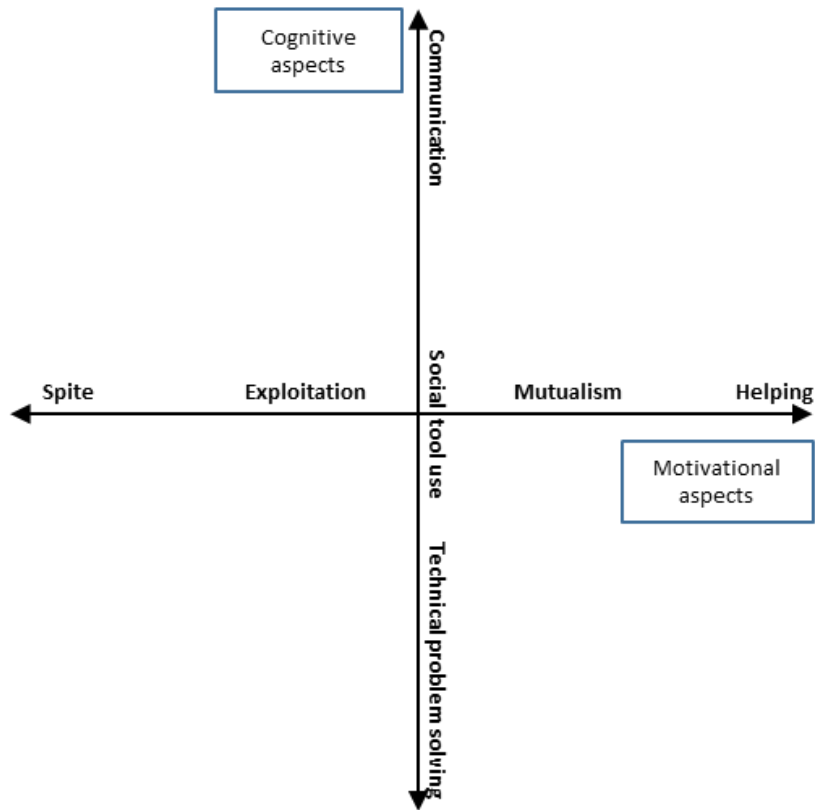
14   social interactions.

15
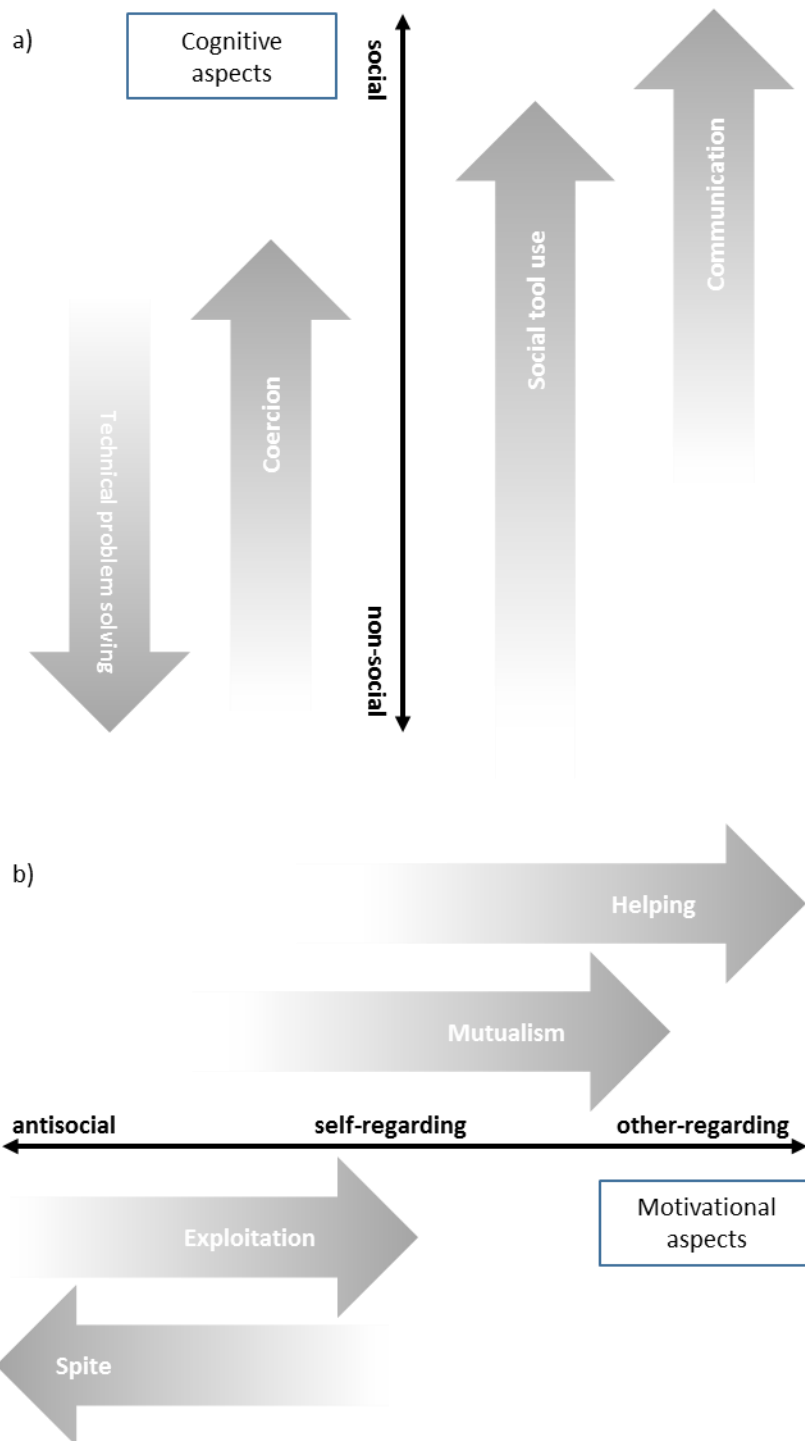
1   Figure 1

2

3

1   Figure 2

2
3

1   Figure 3

2