

## **How much of our cooperative behavior is human?**

Brian Hare<sup>1, 2</sup>

Jingzhi Tan<sup>1</sup>

<sup>1</sup> Duke University, Department of Evolutionary Anthropology, Box 90383,  
Durham, NC 27708

<sup>2</sup> Duke University, Center for Cognitive Neuroscience, B246 Levine Science  
Research Center, NC 27708

**Word Count: 6,441**

## **Abstract**

Observational studies on primates – and in particular chimpanzees and bonobos – have uncovered a number of joint activities that these species engage in and suggest that our closest relatives might also possess sophisticated skills that allow for flexible forms of cooperation. By experimentally presenting different cooperative tasks to chimpanzees and bonobos we have learned that their naturally occurring cooperation is likely explained by an ability to collaborate together with motivation to help – at least in some contexts. Moreover, it is likely that apes have the potential to escape the costs associated with active punishment in maintaining long-term cooperative relationships by simply shunning non-preferred social partners. The same research has also revealed that contingent reciprocity likely plays a limited role in maintaining nonhuman ape relationships while tolerance significantly constrains cooperative flexibility in nonhumans. This is an exciting moment as researchers continue to develop paradigms that show cognitive limitations in experimental contexts where apes are already known to successfully cooperate. In this way we will truly learn what is human about our cooperative behavior.

Whether it is our technological, cultural, institutional or linguistic capabilities almost every behavior that we might call “human” is ultimately a product of cooperation. Characterizing human cooperation and explaining its evolution will be central to explaining the evolution of our species. One of the tools we have available for testing hypotheses regarding human cooperation is the comparison of cooperative abilities among hominoids. Humans share a common ancestor with the *Panins* (bonobos and chimpanzees) some 5-7 million years ago. In comparing our own species with bonobos and chimpanzees we can identify traits we share and those that arose as derived traits during human evolution. Therefore, comparisons between the cooperative behavior of chimpanzees, bonobos and humans allow us to test hypotheses regarding the unique nature of human cooperation. We review a number of studies on chimpanzee and bonobo cooperation in recent experiments that simultaneously help explain the cooperative behavior they demonstrate in the wild while also testing hypotheses about the unique nature of human cooperation.

### **Preconceptions and observations of ape cooperation**

We now know so much about wild bonobos and chimpanzees that it is easy to forget that the first long-term research on wild ape behavior began less than 50 years ago. This means for 90 years after the publication of *The Origin of Species*, little, if anything, was known about the naturally occurring behavior of apes. Because the first attempt to study wild chimpanzees in French Guinea was very short lived (Nissen, 1931), the majority of information on chimpanzee behavior was provided by the pioneering work of Robert Yerkes and Wolfgang Koehler

with small captive populations of young chimpanzees (Koehler, 1925; Yerkes & Yerkes, 1929), As a result, while knowing that chimpanzees were highly social, before the early 1970s little else was understood about the character of chimpanzee social life. Based on such scant information some in this period suggested chimpanzees might only show cooperative behavior in experiments conducted in captivity.

“Nissen has made the point, however, that in the native habitat, where the necessities for life are very easy to obtain (food, water, simpler shelter, and protection from enemies), the chimpanzee’s full capacities are not taxed to the limit. The necessity for well integrated cooperative activity in order to satisfy biological needs perhaps has never arisen, and hence in the field one should not expect to see the type of team work which might be demonstrated in the laboratory, where such behavior could be put at a premium (Crawford, 1937, p 4)”.

Therefore, before fieldworkers began to unlock the secrets of chimpanzee social life, few might have guessed the extent to which chimpanzee survival and reproduction depends on their ability to work together with other group members in a variety of contexts. We now know that chimpanzees and bonobos cooperate in a wide range of situations in the wild and that they show a fair amount of plasticity in their cooperative behaviours across a range of ecologies (see Muller and Mitani, 2005 for a comprehensive review). For example, both

bonobos and chimpanzees have long term relationships in which they support each other through grooming, coalitionary support and food sharing (de Waal, 1982; 1997; Nishida, 1983; Goodall, 1986; Kano, 1992; Parish, 1994; Vervaecke et al, 2000; Watts, 2002; Hohmann and Fruth, 2002). In addition, male chimpanzees have been observed to regularly hunt monkeys and patrol their territory borders in groups. (Nishida, 1979; Wrangham, 1999; Boesch & Boesch-Achermann, 2000; Watts & Mitani, 2001; Mitani & Watts, 2001; Williams et al, 2004)

The variety, frequency, adaptability of *Panin* cooperation along with the reduced role of kinship in explaining it (e.g. Gerloff et al, 1999; Langergraber et al 2007) raise many questions regarding the underlying motivation and cognitive skills that allow for (or constrain) these species cooperative behavior. The flavour of the questions are the same: is it that *Panin* cooperation is a by-product of individuals egocentrically pursuing their own interest with little understanding of how their success depends on the behavior of others or is it that nonhuman apes have a richer understanding of the social nature of their joint successes (Boesch, 1989; Watts & Mitani, 2002; Noe, 2006). Do they know when they or someone else needs help? Can they work together with anyone within their group? Do they know that some group members are better helpers than others? Will they only help if it is a mutualistic endeavour or is their helping sometimes more costly in nature? Will they help a stranger? Can they detect, shun or even actively punish cheaters?

It is here that experiments will make an important contribution to our understanding of *Panin* cooperation. Many of the questions above are very difficult to answer without careful experimentation in addition to detailed

observations. For example, because observation conditions can be so difficult during hunting there is disagreement regarding the psychology that might underlie this behaviour. In this case it may be most productive to examine the collaborative potential of chimpanzees in the laboratory (Muller & Mitani, 2005; Mitani, 2006). So while Nissen and Crawford's initial speculation regarding the extent to which chimpanzees cooperate has proven incorrect, the spirit of Crawford's suggestion that laboratory work will be crucial for the study of chimpanzee cooperation is indeed valid. It is now the job of experimentalist to test how flexibly the natural cooperative skills of *Panins* generalize to novel (and sometimes artificial) situations. This way we should be able to expose not just the cooperative potential of other apes, but also their limitations.

### **Experimental investigations of cooperation**

Although chimpanzees and bonobos have been observed to cooperate in a diverse number of contexts until recently there has been little experimental evidence to support the idea that their cooperation relies on sophisticated cognitive mechanisms. When given a novel instrumental task that required joint action (i.e. pulling a heavy tray baited with food) chimpanzees had to be explicitly trained to solve the problem and the newly learned cooperative skills did not generalize to a slightly different cooperative task (Crawford, 1937; 1941; Savage-Rumbaugh et al, 1978; Chalmeau, 1994; Povinelli & O'Neill, 2000). However, in all of these previous experiments a handful of chimpanzees were tested, no bonobos were studied, and the performance of the chimpanzees seemed constrained by intolerance between potential partners (Chalmeau, 1994). This

suggests that larger samples of subjects from both species where social relationship variables can be measured and controlled might provide an opportunity to observe spontaneous cooperation in captivity while gaining insight to its evolution.

### *Tolerance and cooperation*

Work with other non-ape species has demonstrated that the ability to cooperate is constrained by tolerance (Petit et al. 1992; Chalmeau 1994; Mendres & de Waal 2000; Visalberghi et al. 2000; Werdenich & Huber 2002; de Waal & Davis, 2003; Seed et al, 2008). Thus, one possible explanation for the discrepant findings between observational and experimental studies of chimpanzee cooperation is that non-cognitive factors constrain the ability of chimpanzees to cooperate in experimental settings (e.g. Chalmeau, 1994). A number of studies with *Panins* now support this hypothesis.

Melis et al (2006a) presented a novel instrumental task to sixteen pairs of chimpanzees but only after testing them for their ability to share food. Once the level of food-tolerance within each pair was assessed a long platform was placed in front of their testing room but out of their reach. Food was placed in two separate piles on either side of the food platform. A single rope was threaded through two different loops on either end of the food platform so that the food tray could be retrieved if both ends of the ropes were pulled simultaneously. If the rope ends were spread beyond the reach of a single individual then success in retrieving the food requires cooperation. However, pulling one of the rope ends will only pull the rope out of the loops like a shoe string in a shoe – resulting in

failure (because this apparatus was initially designed by Hirata, 2003, we will hereafter refer to it as the Hirata paradigm). When pairs in each dyad were released simultaneously many spontaneously solved the problem, and their performance in a single six trial session correlated with their feeding-tolerance score from the pre-test. Moreover, individuals from pairs with intolerant dyads were repaired with individuals they were tolerant with and subsequently solved the same problem almost immediately. The reverse was also done with the initial tolerant pairs with the opposite effect. They no longer could solve the problem they had already previously been capable of solving with a tolerant partner.

Melis et al (2006a) provides direct evidence that chimpanzee cooperation is highly constrained by inter-individual tolerance levels and also suggests that species differences in tolerance may explain variance in cooperative abilities across species (including that seen in humans compared to other animals). In order to test this hypothesis Hare et al (2007) replicated the previous method with a group of bonobos and directly compared their performance to chimpanzees. In the tolerance tests bonobos proved to be more tolerant than chimpanzees showing higher levels of socio-sexual and play behavior (also see Palagi, 2006). Importantly, the higher level of socio-sexual behavior seen in bonobos was largely due to the complete absence in chimpanzees. Bonobos had a socio-sexual interaction in only one of six trials on average. But chimpanzees simply avoided physical contact in this context. Bonobos were then compared to chimpanzees in the Hirata pulling paradigm in six trials. Crucially, the age and sex of the subjects from both species were carefully matched to control for the effect of these variables. The two species were equally skillful at cooperating to

retrieve the food when food was placed as in Melis et al (2006a) with two separate food piles at either end of the food platform. However, in a second condition when food was only placed in a single pile in the center of the food platform the bonobos outperformed the chimpanzees. This was also the case when subjects were repaired with a new cooperative partner in another round of six trials. When food was easily monopolizable the more tolerant species was more skillful at cooperating with multiple partners – even though the chimpanzees tested were very experienced with the task and the bonobos were completely naïve before testing (i.e. in fact, the chimpanzees tested here had previously participated in Melis et al, 2006b; 2009, described below). Tolerance is such a powerful constraint that even individuals who are expert at the cooperation task cannot solve it when they perceive food as monopolizable.

The species differences found in Hare et al (2007) suggest that bonobos and chimpanzees differ in their ability to cooperate as a result of tolerance constraints on chimpanzees. Thus, understanding the mechanism allowing for these species differences in tolerance will help us to understand how ape cooperation evolves. Comparisons of the physiological response during dyadic food sharing trials reveal differences in males of the two species in particular. Wobber et al (submitted) found that when a pair of chimpanzee males is unable to share food they show an increase in testosterone but not cortisol in anticipation of being released together into a room full of food. This response is consistent with being primed for a competitive social interaction and avoidance of physical contact (Salvador & Costa, 2009). In contrast, male bonobos who are unable to share show a dramatic anticipatory increase in cortisol but not

testosterone (see also Hohman et al, 2008). This response is consistent with a coping style that promotes social interactions in the face of competition that might reduce stress (i.e. play and socio-sexual behavior). Wobber et al (2010) also tested the hypothesis that higher levels of feeding tolerance in bonobos result from a shift in the development of their social psychology. Bonobos and chimpanzees ranging in age from young juveniles to adults were again tested for their ability to share food. Subjects of both species were tested in age matched dyads that controlled for sex. Bonobos again were more tolerant than chimpanzees showing more play and sex behavior, but in addition an interesting developmental pattern was revealed. While both chimpanzee and bonobo juveniles are equally tolerant, chimpanzees become increasingly intolerant as they age while bonobos maintain juvenile levels of tolerance into adulthood. Wobber et al (2010) also showed that in two contexts simulating feeding competition chimpanzees developed inhibitory control skills at a much younger age than bonobos. Even adult bonobos were less inhibited than adult chimpanzees when begging for food.

Taken together, the results show how tolerance can constrain cooperation even in individuals who understand a great deal about the cooperative problem they must solve. Comparisons between *Panins* show that species differences in cooperation can be a result of differences in tolerance and that developmental shifts in social psychology and differential physiological reactivity play a role in mediating these species differences in tolerance. Therefore, one of the first changes that had to occur to promote human levels of cooperation in our own species evolution is an increase in tolerance. Selection may have acted on the

development of our social psychology and physiology to produce a more tolerant hominid that could then more flexibly apply its cooperative skills (Hare, 2007).

### *Collaboration*

There remains considerable controversy around the question of what degree chimpanzee hunting (or any other form of cooperation) depends on coordinated and intentional collaboration or a simpler mechanism such as joint action in which multiple individuals pursue the same goal independently but simultaneously (Tomasello & Call, 1997; Boesch & Boesch-Achermann, 2000; Muller & Mitani, 2005; Noe, 2006). Moreover, while some have emphasized the strategic nature of chimpanzee meat sharing other evidence suggests that sharing is used as a technique to reduce harassment and piracy by other chimpanzees (Gilby 2006; see also Hohman & Fruth, 2002).

In order to test between the rich and lean interpretations of the naturally occurring cooperative behavior of chimpanzees, Melis et al (2006b) tested whether chimpanzees understood the role of their partner in their success in the Hirata pulling task. In retrieving the food in Melis et al (2006a) chimpanzee dyads could succeed if they were simultaneously attracted to and willing to pull one of the two rope ends. Like observations of wild cooperation they may have simply solved the problem through joint action without an understanding of their partner's role. Therefore, Melis et al (2006b) released only one individual from a highly tolerant pair of chimpanzees into a testing room. Their potential partner was locked in an adjacent room with a one-way key that only the subject could remove to free her partner. All subjects had previously learned they could open

the door to enter the adjacent room to retrieve food, but they had never been shown they could open the door for another chimpanzee. Instead of pulling the rope out of the food platform and failing to retrieve the food, the subjects spontaneously opened the door for their partner and waited until they arrived before they pulled in the platform together successfully. In a control in which the two rope ends were placed close together so that the subject did not need help in retrieving the food, the subjects did not release their partner from the room. Therefore, chimpanzees do spontaneously show an appreciation of the role of another individual in their success solving a novel instrumental task. Chimpanzees were able to use another chimpanzee as a social tool when they needed help solving a problem, but avoided using their help when they were not needed (i.e. receiving all the food).

Recognizing the utility of a social partner is just one component of collaboration, because collaborators must also find a way to cooperate even when interests may initially conflict. Melis et al (2009) tested the ability of highly tolerant pairs of chimpanzees to negotiate when the payoffs from mutual effort are potentially unequal. Pairs of tolerant chimpanzees were now faced with the choice of retrieving an out-of-reach food platform with equal payoffs for each or a platform that had the same amount of food as the other but distributed unequally on either end of the platform. The more dominant in each pair was then released to make an initial “offer” by sitting in front of one of the four food dishes at the end of each platform while holding the rope. Shortly after, the subordinate of the pair was then released to either accept the offer by pulling the other end of the same rope or to make a “counteroffer” by sitting in front of another food dish on

the other food platform. The dominants tended to offer the unequal split and subordinates then refused to accept this offer in the majority of trials. However, if the chimpanzees understand they needed each other to obtain the food they should be able to “negotiate” a compromise. Perhaps remarkably, subjects were able to quickly come to an agreement and successfully cooperate in almost 90% of trials. Moreover, in the majority of trials where dominants initially offered the unequal split the dyad ended up retrieving the food platform with equal payoffs. Crucially, if the dominant accepted the subordinates’ counteroffer of the equal payoff, the subordinate did not then attempt to counteroffer the unequal platform in order to obtain the largest food payoff. Therefore, both individuals recognized that the other possessed leverage and recognized the limits of their own power in this situation.

Taken together, these two studies show that semi-captive chimpanzees are capable of spontaneously and flexibly collaborating (no experiments have been conducted with bonobos). Given that wild chimpanzees have decades to practice hunting and forming alliances, it seems that skills revealed in the experiments are likely used ubiquitously in the natural interactions of chimpanzees. This may account for novel cooperative behaviors that have been observed in wild populations such as guarding during street crossings at Bossou (Hockings et al, 2006). However, there are limits to the collaborative abilities of chimpanzees. For example, while a pair of chimpanzees learned to solve the Hirata paradigm by recruiting the help of a human, they were unable to spontaneously recruit a human to help them pull a heavy object Hirata & Fuwa (2007). Experiments will help us reveal more about the constraints as well as the potential chimpanzees

have as collaborators. In turn we will gain insight about how our species collaborative skills built on those observed in other apes, but now surpass them in terms of their flexible application.

### *Costly cooperation*

All of the cooperation experiments described thus far resulted in a beneficial outcome for both the subjects tested. Bonobos and chimpanzees in their natural interactions also share prized food items and support each other in conflicts with conspecifics and predators. These types of behaviors can potentially be costly not just energetically but also towards an actor's inclusive fitness. One hypothesis suggest that this type of helping is egocentrically motivated while others have argued that helping is more pro-social in nature (Silk et al, 2005; Gilby, 2006; deWaal, 2007).

In order to understand the psychology behind the seemingly costly behavior of chimpanzees and bonobos in their natural interactions several experiments have been conducted to examine the pro-social tendency of chimpanzees and bonobos. Initial experiments examining chimpanzee food sharing preferences support the view that much sharing that is observed in their natural interactions occurs in attempts to reduce the cost of harassment and does not result from a preference for sharing (Silk et al, 2005; Jensen et al, 2006; Vonk et al. 2008). In these studies chimpanzees did not prefer to retrieve a food tray that provided food both to them and to a different room with another chimpanzee. Instead, they chose randomly between the option providing food to two rooms over another option where they would receive the same amount of

food but the other chimpanzee would receive nothing. These findings have, in part, led some to suggest that the pro-social tendency seen in humans is derived and potentially evolved together with another social trait such as our shift to cooperative breeding (Burkhart et al, 2007). However, none of these initial studies successfully demonstrated in a pretest that the subjects understood the physical properties of the task. It is necessary to demonstrate that when tested alone subjects prefer the option where food is provided in two rooms if they themselves are allowed to retrieve all the food. Otherwise a null result in the test is likely due to subject's failure to understand the physical set-up. Unfortunately, these crucial controls were only run in one study and when run they did not work (e.g. Jensen et al, 2006, experiment 1). Moreover, when human infants were tested in the same contexts they did not consistently show a prosocial tendency (Bronwell et al, 2009). Therefore, until the appropriate controls are run it is difficult to make strong conclusions from this test situation (note: in experiment 2 of Jensen et al 2006 the controls worked and two subjects did show a pro-social tendency).

Because of the limitations of the food tray tasks, Warneken et al (2007) used a new helping paradigm to test the motivation and skills of chimpanzees that was based on tasks previously validated with children (Warneken & Tomasello, 2006). While a chimpanzee watched, a human was playing with a toy. Another experimenter then came and stole the toy and placed it out of the other person's reach but within reach of the chimpanzee. The question was whether the chimpanzee would return the stolen toy to the human who had previously been playing with it. Regardless of whether the chimpanzee was rewarded with

food for returning the toy or not, the chimpanzees repeatedly helped the human. Across ten trials there was no decrease in helping even though the chimpanzee was repeatedly requested to help without receiving a food reward. They even helped in a condition where retrieving the toy required climbing several meters into a tunnel before bringing it back to the human. When the exact same procedure was run with young infants, there was no species difference in the level of helping. Thus, when tested in the same situation (that did not require understanding the physical properties of an apparatus) chimpanzees are as helpful as human children.

Although the previous experiment shows chimpanzees help humans, it is possible they are not motivated to help other chimpanzees. Therefore, Warneken et al (2007) designed another study in which a chimpanzee could potentially release another chimpanzee into a food room that they themselves did not have access too. The subject had previously learned that if they pulled a key, they themselves could obtain food by passing from the room with the key, into a second room where they could then open the door into the food room. They also had learned that if they were locked into the room with the key they could not obtain the food even if they pulled the key that freed the door between the second room and food room. This means before being tested Warneken et al (2007) demonstrated their subjects understood the physical properties of the task making it easier to interpret a positive or negative result as a valid measure of helping. In the test subjects were locked in the key room and could choose to open the door for a recipient in the second room or ignore them. Subjects opened the door into the food room for the recipient in the majority of experimental

trials with no decrease in opening across trials. They also opened in the experimental condition more often than the control when opening did not help the recipient obtain food (i.e. food was not placed in the food room). The subject could easily see the recipient obtain and eat the food (although in each trial it was placed out of the subjects view) and recipients never shared their food with the subject. Importantly, there was no way for recipients to physically harass subjects. Therefore, subjects repeatedly gave another chimpanzee access to food even though they received no reward for doing so. Studies on a variety of other primates suggest that it is not nonhuman apes alone who help in such ways (Burkhart et al, 2007; Lakshminarayanan & Santos, 2008; Cronin & Snowdon, 2007; deWaal et al, 2008)

Although chimpanzees helped others in Warneken et al (2007) subjects never “have to sacrifice their own rewards to provide rewards to others (Silk, 2008, p. 279).” Subjects had to either retrieve an object or give access to food they could not obtain. While this shows a willingness to help another individual - it is low-level helping in the sense that the costs are relatively low to the actor. Therefore, helping observed in this experiment likely does not simulate the costs associated with actively sharing meat or other high quality food. Moreover, it is unlikely that chimpanzees would sacrifice their own food given the results of Melis et al (2006b; 2009). In one experiment chimpanzees avoided opening a door when they did not need the help of the partner (i.e. so they could eat all the food, Melis 2006b). In another experiment, dominant chimpanzees almost never offered the larger amount of food on the unequal food tray to their subordinate partners (Melis et al, 2009). Meanwhile, humans often publically distribute food

they have collected to others in their groups (Boehm, 1999; Hill, 2002). This might suggest high cost food sharing is uniquely humans, but it is difficult to come to any conclusions about the evolution of human food sharing without experimentally examining bonobos. Therefore, Hare & Kwetuenda (2010) gave bonobos the opportunity to either monopolize food or to open a door and share part of their food with a conspecific. We found that bonobos preferred to release a recipient from an adjacent room and feed together instead of eating all the food alone. They shared with another bonobo even though they ate all of the food alone in a control when given the same amount as used in the test. Over ten trials bonobos continued to voluntarily share their food allowing the recipient to feed during 80% of the total feeding time needed to eat all the food provided. The sharing cannot be explained by 1) harassment, since recipients could not approach the food without the subject's help, 2) kinship, since none of the subjects were related and 3) attempts by subjects to reciprocate previous favors, since subjects even shared with recipients who were non-group members. Therefore, subjects preferred to voluntarily open the recipient's door to allow them to share highly desirable food that they could have easily eaten alone – with no signs of aggression, frustration or change in the speed or rate of sharing across trials. This stable sharing pattern is particularly striking since in other non-sharing contexts bonobos are averse to food loss and adjust to minimize such losses (e.g. Wobber et al, 2010). More work is clearly needed to understand more precisely how human helping and sharing might differ from that seen in chimpanzees and bonobos. While humans and Panins will certainly differ in this respect, the differences are likely to be more nuanced than initially hypothesized.

### *Maintaining cooperation*

Whether a cooperative relationship is based on mutualism or a more altruistic exchange there must be a mechanism by which cooperation is maintained. However, it has been suggested reciprocal altruism will be rare in nature because of the high rate of discounting in animals and a lack of inhibitory control (Stevens & Hauser, 2002). It has also been suggested that humans have a unique motivation to pay a cost in order to punish a cooperator who defects (Fehr and Gächter, 2002). It may be that calculated reciprocity and active punishment play an important role in allowing for unique forms of human cooperation. Meanwhile, there is abundant evidence for reciprocal exchange of grooming, coalitionary support, and food sharing in chimpanzees and bonobos. Moreover, the reciprocal exchanges seen in philopatric wild male chimpanzees cannot be explained by kin relations (Langergraber et al, 2007). Given that Panins have reciprocal relationships, experimenters have begun exploring what cognitive mechanism might allow for and constrain chimpanzee reciprocity (no experiments have been conducted with bonobos).

First, Melis et al (2006b) used the Hirata paradigm to test if chimpanzees can distinguish between a skilled and unskillful cooperative partner. Two potential partners were positioned in two separate rooms that were adjacent to the testing room. In pre-tests one potential partner demonstrated skill with the Hirata apparatus while the other always immediately caused a failure by pulling the rope without his pre-test partner. Moreover, although all subjects were highly tolerant with both potential partners, no subject had ever been paired with either

partner to solve the cooperation task. In the test a subject was released into the testing room where the rope from the out-of-reach food tray was positioned. Subjects could then choose with which partner to solve the cooperation problem by removing one of the one-way keys that locked the door between one of the adjacent rooms and test room. Subjects initially did not have a preference between the two potential partners in the six trial introduction. However, trial-by-trial analysis revealed that subjects did use a win-stay lose-shift strategy in the introduction. Subjects preferred to open the door for a partner if the choice of that partner on the previous trial had led to success. Likewise, they switched partners on a trial following failure. Perhaps most remarkably, in the six trial test session that was conducted as much as a week after the introduction, subjects almost exclusively chose the more skillful partner. This study demonstrates that chimpanzees develop and encode a reputation about the cooperative skill level of different individuals for a significant period of time. Social memories of this kind could provide a foundation for reciprocal relationships. It also suggests that chimpanzees are capable of maintaining cooperative relationships through shunning. This highly effective, low-cost form of punishment does not require physical contact that can lead to injury. Instead, in a fluid fission-fusion society individuals can completely escape the dilemma of the second order cost of punishment by simply avoiding problematic conspecifics in favor of beneficial social partners (Barrett et al, 1999).

The ability of chimpanzees to quickly assess the skill of another chimpanzee and to encode this information suggests their reciprocal relationships could be based on the memory of previous social interactions.

Melis et al (2008) used two experimental techniques to examine whether six dyads of chimpanzees are capable of calculated reciprocity. The first experiment was based on Melis et al (2006b) in which a subject could choose to open a door and cooperate together with a partner who had chosen to cooperate with them or a partner that had avoided choosing them as a cooperative partner. The second experiment was based on Waneken et al (2007) in which the subject could choose between releasing another chimpanzee into a room with food that had previously released them or another chimpanzee who had refused to release them. In both experiments there was a significant but weak tendency for chimpanzees to choose the individual who had chosen them before. This suggests that with a larger sample it may be possible to demonstrate calculated reciprocity (although note that a larger sample was not needed when the same subjects were tested in Melis et al 2006a,b; 2009 and Waneken et al 2007). However, a number of other experiments have revealed little evidence for contingent reciprocity. In many of these studies chimpanzees needed to exchange tokens with one another in order to obtain food but in these contexts reciprocal exchanges either quickly breakdown or never develop (Brosnan & Beran 2009; Dufour et al. 2008; Pelé et al. 2009; Yamamoto & Tanaka 2009a; 2009b; Yamamoto et al. 2009). Finally, in Melis et al (2009) in which chimpanzees negotiated conflicting interests, a condition was run in which the food platform with unequal amounts of food had nearly twice as much food as the equal platform. In this situation the most advantageous strategy is to reciprocally take turns receiving the largest food pile on the unequal platform. In this way both individuals receive more food than if they only are able to agree on the platform with equal payoff. The chimpanzees did not

develop a reciprocal strategy in this situation although they were still very successful at agreeing to retrieve one of the two platforms (i.e. when they agreed to pull the unequal tray the dominant always received the larger payoff; see also Brosnan et al. 2008; Yamamoto & Tanaka in press).

Overall the picture regarding nonhuman ape reciprocity remains cloudy. While chimpanzees and bonobos clearly have reciprocal relationships experimental methods have yet to be developed that provide the most powerful test possible. In the one context in which chimpanzees seem to potentially show contingent reciprocity the sample size could be characterized as relatively small (N=6 dyads). Moreover, bonobos have never been tested in a test of reciprocity. Therefore, it is still possible that future experiments will find evidence for contingent reciprocity (and perhaps even calculated reciprocity since *Panins* have low discounting rates, are skilled at simple arithmetic, and have shown impressive inhibitory control in a number of cooperative tasks; Rosati et al, 2007; Hanus & Call, 2006; Melis et al, 2006b; 2009). However, based on the current evidence, it seems most likely that symmetry within chimpanzee relationships is based on attitudinal reciprocity or long term relationship factors that cut across currencies (Melis et al, 2008). Even if calculated reciprocity is demonstrated, it likely plays a minor role in maintaining cooperation within *Panins*. In addition, we predict that chimpanzees will avoid direct conflict when cooperation breaks down and simply shun unprofitable social partners. Humans, then, may have additional mechanism for the maintenance of cooperation that are not found in the *Panins*, but it will be important to demonstrate why attitudinal reciprocity and shunning cannot explain the cooperation we see in our species.

### ***Going wild with captive cooperation***

Anytime we observe a behavior it can have multiple mechanistic explanations regarding the underlying psychology that produces it. Experiments allow us to probe these mechanisms and test between different hypotheses that cannot be tested using observational techniques alone. Based on the newest experiments reviewed above, we now know that a major constraint on cooperation is tolerance. Almost certainly during human evolution there was a major shift in tolerance levels that allowed for more forms of joint activity that could then develop into collaborative endeavors. We also now know that chimpanzees are capable of spontaneously and actively recruiting a collaborative partner when faced with a novel problem that requires cooperation. They also can assess the leverage they have in deciding which cooperative problem they wish to solve. This suggests that wild chimpanzees are capable of recruiting alliance partners in social competitions and when hunting. It also suggests they have some understanding that cooperation changes the balance of power within the cooperative dyad itself and not just between those within the alliance and those outside it (i.e. they realize they need each other, which reduces the asymmetry in the relationship). We have also observed that not all food sharing between apes is likely explained by harassment. Chimpanzees will help another retrieve an object or food even if no reward is given in return. Meanwhile, bonobos in some contexts prefer to share food rather than simply eat it all alone. This type of sharing is of relatively high cost, likely due to pro-social motivations and may explain the increased gregariousness in this species. Finally, studies of

mechanisms maintaining cooperation have shown that chimpanzees can shun unskillful cooperators but there still remains only weak evidence for contingent reciprocity. Therefore, we suspect that simpler mechanisms such as attitudinal reciprocity that can rely on low-cost punishment in the form of shunning maintain most cooperative relationships in apes.

Based on all the research just describe it would be easy to think that Crawford (1937) was completely misguided for ever thinking that cooperative behavior might emerge in laboratory experiments that was not already observed in the natural behavior of chimpanzees. However, this is exactly what we have found in studying the behavior of ape cooperation in the lab: apes can flexibly adapt their cooperative behavior in completely novel situations. First, recall that there is very little evidence that female chimpanzees actively cooperate in the wild. Although there is variance in general it is males and not female chimpanzees that work together in seemingly complex ways. However, a significant number of females were extremely skilled in our tasks (Melis et al, 2006a,b; 2008; 2009). It seems that females living in a rich environment when paired together with a highly tolerant partner have as sophisticated skills of cooperation as those seen in male chimpanzees. Second, even though bonobos have never been observed to cooperate in many of the ways observed in wild chimpanzees, they are more skilled than chimpanzees in the Hirata pulling task if the food reward in the experiment is highly monopolizable (Hare et al, 2007). It seems that the higher levels of food tolerance in bonobos allow them to outperform chimpanzees in some cooperative tasks in captivity even though they never obtain food through joint effort in the wild (i.e. arguably supporting Nissen

and Crawford's initial idea that a rich and predictable environment may not promote cooperative behavior that then might be expressed in the lab).

We highlight these examples because there has often been tension between those studying wild primates using observational methods and those in captivity using more experimental methods. Both approaches have much to offer if we want to understand the full range of behavioral flexibility. Just as we would have never known that chimpanzees can hunt in groups without field studies we would never have known how skilled female chimpanzees and bonobos are in collaborative activities without experimental studies in captivity. Ultimately we want to know the range of flexibility apes show when cooperating and an accurate assessment requires observing these species in as many contexts as possible. Even after considering ape cooperation across all contexts, what remains puzzling is the fact that there is substantial evidence they possess cognitive skills that allow for mutualistic endeavors, but this flexibility remains limited to a few contexts in comparison to what is observed in humans. We suspect that it is not an altruistic tendency that makes humans unique, but instead an ability to recognize the potential benefit of mutualistic endeavors in a wide range of situations (allowing humans to avoid the need to be altruistic). After all, there is no puzzle to explain when mutualism evolves. Instead, the puzzle is why we do not see more complicated forms of it outside of humans. This will be the key to understanding both how much of our cooperation is human and how it evolved.

## References

- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J., and Hill, R. (1999). Market forces predict grooming reciprocity in female baboons. *Proc. Roy. Soc. Lond. B* 266, 665-670.
- Boehm, C. (1999). "Hierarchy in the Forest: The Evolution of Egalitarian Behavior." Harvard Univ. Press, Cambridge, MA.
- Boesch, C., and Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *Am. J. Phys. Anthropol.* 78, 547-573.
- Boesch, C., and Boesch - Achermann, H. (2000). "The Chimpanzees of the Tai Forest." Oxford Univ. Press, Oxford.
- Brosnan, S. & Beran, M. 2009. Trading behavior between conspecifics in chimpanzees, Pan troglodytes. 123, 181-194.
- Brosnan, S., Silk, J., Henrich, J., Mareno, M., Lambeth, S., Schapiro, S. (2009). Chimpanzees (Pan troglodytes) do not develop contingent reciprocity in an experimental task. *Animal Cognition*.
- Brownell, C. Svetlova, M., Nichols, S. (2009). To share or not to share: when toddlers respond to another's needs? *Infancy*.
- Burkart, J. Fehr, E., Efferson, E., van Schaik, C. (2007). Other-regarding preferences in a nonhuman primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences*. 104, 19762-19766.
- Chalmeau, R. 1994. Do chimpanzees cooperate in a learning task? *Primates*, 35, 385-392.
- Crawford, M. P. 1937. The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs*, 14, 1-88.
- Crawford, M. P. 1941. The cooperative solving by chimpanzees of problems requiring serial responses to color cues. *The Journal of Social Psychology*, 13, 259-280.
- Cronin, K. and Snowdon, C. (2007). The effects of unequal reward distributions on cooperative problem solving by cotton-top tamarins. *Animal Behaviour*. 75, 245-257.
- de Waal, F. (1982). "Chimpanzee Politics." Harper and Row, New York.
- de Waal, F. (1997). The chimpanzee's service economy: food for grooming. *Evol. Hum. Behav.* 18, 375-386.
- de Waal, F. B. M. & Davis, J. M. 2003. Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychologia*, 41, 221-228.
- de Waal, F. & Berger, M. (2000). Payment for labor in Capuchin monkeys. *Nature*. 404, 583.
- de Waal, F., Leimgruber, K., Greenberg, A. (2008). Giving is self-rewarding for monkeys. *Proceedings of the National Academy of Sciences*. 105, 13685-13689.
- De Waal, F. (2007). Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology*. 59, 279-300.
- Dufour, V., Pele, M., Neumann, M., Thierry, B., Call, J. (2008). Calculated reciprocity after all: computation behind token transfers in orangutans. *Biology Letters*.
- Fehr E, Gächter S (2002) Altruistic punishment in humans. *Nature* 415: 137-140.
- Fruth, B., and Hohmann, G. (2002). How bonobos handle hunts and harvests:

- Why share food? In Behavioral Diversity in Chimpanzees and Bonobos. C. Boesch, G. Hohmann, and L. Marchant, eds. (Cambridge, UK: Cambridge University Press), pp. 231–243.
- Gerloff, U., Hartung, B., Fruth, B., Hohmann, G., Tautz, D. 1999. Intra-community relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proc. Roy. Soc. Lond. B* 266, 1189-1195.
- Gilby, I. C. 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour*, 71, 953-963.
- Goodall, J. (1986). "The Chimpanzees of Gombe." Belknap Press, Cambridge, MA.
- Hanus, D., & Call, J. (2007). Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): The effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology*, 121(3), 241–249.
- Hare, B. 2007. From nonhuman to human mind: what changed and why. *Current Directions in Psychological Science*. 16, 60-64.
- Hare, B. & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology*.
- Hare, B., Melis, A. P., Woods, V., Hastings, S. & Wrangham, R. 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, 17, 619-623.
- Hill, K. (2002). Altruistic cooperation during foraging by the ache, and the evolved human predisposition to cooperate. *Human Nature* 13, 105-128.
- Hirata, S. 2003. Cooperation in chimpanzees (in Japanese). *Hattatsu*, 95:103-111.
- Hirata, S. & Fuwa, K. 2007. Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates*, 48, 13-21.
- Hockings, K.J., Anderson, J.R. and Matsuzawa, T. (2006). Road crossing in chimpanzees: A risky business. *Current Biology*, 16 (17), 668-670.
- Hohmann G, Mundry R, Deschner T (2008) The Relationship Between Socio-Sexual Behavior and Salivary Cortisol in Bonobos: Tests of the Tension Regulation Hypothesis. *American Journal of Primatology* 70, 1-10.
- 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.
- Köhler W (1925) The mentality of apes. London: Routledge and Kegan Paul.
- Langergraber, K. E. , Mitani, J. C. & Vigilant, L. 2007. The limited impact of kinship in cooperation in wild chimpanzees. *Proc Natl Acad Sci USA*, 104(19) 7786-7790
- Lakshminarayanan, V. & Santos, S. (2008). Capuchin monkeys are sensitive to others' welfare. *Current Biology*, 18, R999-R1000.
- Melis, A. P., Hare, B. & Tomasello, M. 2006a. Engineering Cooperation in Chimpanzees: Tolerance Constraints on Cooperation. *Animal Behaviour*, 72, 275-286.
- Melis, A. P., Hare, B. & Tomasello, M. 2006b. Chimpanzees Recruit the Best Collaborators. *Science*, 311, 1297-1300.
- Melis, A., Hare, B., Tomasello, M. 2009. Chimpanzees negotiate in a

- bargaining game. *Evolution and Human Behaviour*.
- Mendres, K.A. & de Waal, F.B.M. 2000. Capuchins do cooperate: the advantage of an intuitive task. *Animal Behaviour*, 60: 523-529.
- Mitani, J. (2006). Reciprocal exchange in chimpanzees and other primates. In "Cooperation in Primates: Mechanisms and Evolution" (P. Kappeler and C. van Schaik, Eds.), Springer-Verlag, Berlin.
- Mitani, J., and Watts, D. (2001). Why do chimpanzees hunt and share meat? *Anim. Behav.* 61, 915-924.
- Muller MN, Mitani, JC (2005) Conflict and cooperation in wild chimpanzees. In: Slater, PJB, Rosenblatt, J, Snowdon, C, Roper, T, Naguib, M, editors. *Advances in the Study of Behavior*. New York: Elsevier. pp. 275-331.
- Nissen, H. (1931). A field study of the chimpanzee: observations of chimpanzee behaviour and environment in Western French Guinea. *Comparative Psychological Monograph*, 8, 122.
- Nishida, T. (1983). Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates* 24, 318-336.
- Nishida, T., Uehara, S., and Nyundo, R. (1979). Predatory behavior among wild chimpanzees of the Mahale Mountains. *Primates* 20, 1-20.
- Noë, R. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour*, 71, 1-18.
- Palagi, E. 2006. Social Play in Bonobos (*Pan paniscus*) and Chimpanzees (*Pan troglodytes*): Implications for Natural Social Systems and Interindividual Relationships. *Am. J. Phys. Anthr.* 129, 418-426.
- Parish, A. (1994). Female relationships in bonobos (*Pan paniscus*): Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Hum. Nat.* 7, 61-96.
- Pele, M., Dufour, V., Thierry, B., Call, J. 2009. Token transfers among great apes (Gorilla gorilla, Pongo pygmaeus, Pan paniscus, and Pan troglodytes): species differences, gestural requests, and reciprocal exchange. *Journal of Comparative Psychology*. 123, 375-384.
- Petit, O., Desportes, C. & Thierry, B. 1992. Differential probability of coproduction in two species of macaque (*Macaca tonkeana*, *M. mulatta*). *Ethology*, 90, 107-120.
- Povinelli, D. J. & O'Neill, D. K. 2000. Do chimpanzees use their gestures to instruct each other? In: *Understanding other minds. Perspectives from Developmental Cognitive Neuroscience* (Ed. by Baron-Cohen, S., Tager-Flusberg, H. & Cohen, D. J.), pp. 459-487.
- Rosati, A., Stevens, J., Hare, B., Hauser, M. (2007). The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Current Biology*.
- Salvador A, Costa R (2009) Coping with competition: Neuroendocrine responses and cognitive variables. *Neuroscience and Biobehavioral Reviews* **33**, 160-170.
- Savage-Rumbaugh, E. S., D. M. Rumbaugh, Boysen, S. (1978). "Symbolic Communication Between Two Chimpanzees (*Pan troglodytes*)." *Science*, 201(4356): 641-644.

- Seed, A., Clayton, N. & Emery, N. (2008). Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the royal society B*. 275, 1421-1429.
- Scheid, C & Noe, R. 2009. The performance of rooks in a cooperative task depends on their temperament. *Animal Cognition*.
- Silk J, Brosnan S, Vonk J, Henrich J, Povinelli D, Richardson AS, Lambeth, SP, Mascaró, J, Schapiro SJ (2005) Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437: 1357-1359.
- Silk, J. (2008). Social preferences in primates. In *Neuroeconomics: decision making and the brain*. Eds. P. Glimcher, C. Camerer, E., Fehr, R., Poldrack. Pg. 269-284.
- Stevens, J. , Vervaecke, H., Vries, H., van Elsacker, L. (2005). The influence of the steepness of dominance hierarchies on reciprocity and interchange in captive groups of bonobos (*Pan paniscus*). *Behaviour*. 142, 941-960.
- Stevens, J.R. 2004. The selfish nature of generosity: harassment and food sharing in primates. *Proceedings of the Royal Society of London, Series B*, 21: 451-456.
- Stevens, J. R. and M. D. Hauser (2004). "Why Be Nice? Psychological Constraints on the Evolution of Cooperation." *Trends in Cognitive Sciences*, 8(2): 60-65.
- Tomasello, M., & Call, J. 1997. *Primate cognition*. New York, NY, USA: Oxford University Press.
- Vervaecke, H, de Vries, H., van Elsacker, L. 2000. Function and distribution of coalitions in captive bonobos (*Pan paniscus*). *Primates* 41, 249-265.
- 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*). *Journal of Comparative Psychology*, 114, 297-301.
- Vonk, J., Brosnan, S., Silk, J., Henrich, J., Richardson, A., Lambeth, S., Schapiro, S., Povinelli, D. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*.
- Warneken F, Tomasello M (2006) Altruistic helping in human infants and young chimpanzees. *Science* 311: 1301-1303.
- Warneken F, Hare, B., Melis, A., Hanus, D., Tomasello, M. (2007). Spontaneous altruism in chimpanzees and children. *Public Library of Science*. 5, e184.
- Watts, D. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* 139, 343-370.
- Watts, D., and Mitani, J. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* 138, 299-327.
- Watts, D., and Mitani, J. (2002). Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* 23, 1-28.
- Werdenich, D. & Huber, L. 2002. Social factors determine cooperation in marmosets. *Animal Behaviour*, 64, 771-781.
- Williams, J., Oehlert, G., Carlis, J., and Pusey, A. (2004). Why do male chimpanzees defend a group range? *Anim. Behav.* 68, 523-532.

- Wobber, V. Wrangham, R., Hare, B. (2010). Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology*, 20, 226–230.
- Wrangham, R. (1999). The evolution of coalitionary killing. *Ybk. Phys. Anthro.* 42, 1-30.
- Yamamoto, S. & Tanaka, M. (2010). The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. *Animal Behaviour*.
- Yamamoto, S. & Tanaka, M. 2009. Selfish strategies develop in social problem situations in chimpanzees (Pan troglodytes) mother-infant pairs. *Animal Cognition*. 12, S27-S36.
- Yamamoto, S., Humle, T. & Tanaka, M. 2009. Chimpanzees help each other upon request. *PLoS One*. 4, e7416, 1-7.
- Yamamoto, S., & Tanaka, M. Do chimpanzees spontaneously take turns in a reciprocal cooperation task? *Journal of Comparative Psychology*. 123, 242-249.
- Yerkes, R. & Yerkes, A. (1929). *The great apes: a study of anthropoid life*. New Haven, Yale University Press.