ARTICLE IN PRESS

ELSEVIER

Evolution and Human Behavior xx (2012) xxx–xxx

Evolution and Human Behavior

Original Article

The ontogeny of human prosociality: behavioral experiments with children aged 3 to 8

Bailey R. House[a,*], Joseph Henrich[b], Sarah F. Brosnan[c], Joan B. Silk[a]

[a]Department of Anthropology, University of California, Los Angeles, CA 90024, USA
[b]Departments of Psychology and Economics, University of British Columbia, Vancouver, Canada V6T 1Z4
[c]Department of Psychology, Georgia State University, Atlanta, GA 30302, USA

Initial receipt 8 March 2010; final revision received 27 October 2011

Abstract

Humans regularly engage in prosocial behavior that differs strikingly from that of even our closest living relatives, the chimpanzees (*Pan troglodytes*). In laboratory settings, chimpanzees are indifferent when given the opportunity to deliver valued rewards to conspecifics, while even very young human children have repeatedly been shown to behave prosocially. Although this broadly suggests that prosocial behavior in chimpanzees differs from that of young human children, the methods used in prior work with children have also differed from the methods used in studies of chimpanzees in potentially crucial ways. Here we test 92 pairs of 3–8-year-old children from urban American (Los Angeles, CA, USA) schools in a face-to-face task that closely parallels tasks used previously with chimpanzees. We found that children were more prosocial than chimpanzees have previously been in similar tasks, and our results suggest that this was driven more by a desire to provide benefits to others than a preference for egalitarian outcomes. We did not find consistent evidence that older children were more prosocial than younger children, implying that younger children behaved more prosocially in the current study than in previous studies in which participants were fully anonymous. These findings strongly suggest that humans are more prosocial than chimpanzees from an early age and that anonymity influences children's prosocial behavior, particularly at the youngest ages.

Keywords: Prosocial behavior; Development; Children; Chimpanzees

1. Introduction

Human societies, ranging from traditional small-scale foraging bands to modern nation states, are characterized by extensive cooperation among sizable numbers of individuals. Like other primates, humans show strong nepotistic biases (reviewed by Dunbar, 2008) and develop long-term relationships with reciprocating partners (reviewed by Gurven, 2004). But unlike other primates, we also provide help to unrelated individuals that we do not know and are unlikely to meet again, impose costly punishment on wrongdoers, and adhere to costly group-beneficial social norms (Fehr & Gachter, 2002; Fehr & Fischbacher, 2003; Gintis, Bowles, Boyd, & Fehr, 2003; Fehr & Fischbacher, 2004; Henrich et al., 2005, 2006; Marlowe et al., 2008; Henrich et al., 2010). Such one-shot cooperative interactions between nonrelatives cannot be explained by kin selection (Hamilton, 1964), "direct" reciprocity (Trivers, 1971; Axelrod & Hamilton, 1981), or "generalized" reciprocity (McNamara, Barta, Fromhage, & Houston, 2008). Direct and generalized reciprocity can produce cooperation between repeatedly interacting nonrelatives by trading off the benefits of defecting within a single cooperative interaction with the expected benefits of cooperating across multiple interactions. Cooperation spreads when the benefits to repeated interactions outweigh the benefits to a single defection, but these mechanisms require that partners are able to interact repeatedly. However, "indirect" reciprocity (Nowak & Sigmund, 2005; Alexander, 2006) avoids this need for repeated interactions by requiring instead that individuals have knowledge about the past cooperative behavior of their partners. Indirect reciprocity factors in the benefits of future cooperation with many different partners, whereas direct and generalized reciprocity factors in only the benefits of future

* Corresponding author. Department of Anthropology, University of California-Los Angeles, Box 951553Los Angeles, CA 90095-1553.
E-mail address: bhouse80@ucla.edu (B.R. House).

1090-5138/$ – see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.evolhumbehav.2011.10.007

cooperation with previous cooperative partners. As such, indirect reciprocity can maintain cooperation even in one-shot interactions. If human cooperation were maintained solely by mechanisms such as indirect reciprocity, humans' economic decisions ought to be dictated entirely by what maximizes our individual payoffs. Yet surprisingly, a large body of experimental evidence from economics and psychology reveals that people have preferences for outcomes that benefit others (hereafter, "prosocial outcomes") which are sometimes strong enough to motivate decisions that conflict with individual self-interest (Batson, 1991, 1987; Batson, Duncan, Ackerman, Buckley, & Birch, 1981; Fehr & Fischbacher, 2003), although the strength of these preferences varies substantially among populations and across contexts (Henrich et al., 2005, 2006, 2010).

Interest in the selective forces that favored the evolution of prosocial preferences in humans (Bowles, 2006; Bowles & Gintis, 2004; Boyd, Gintis, Bowles, & Richerson, 2003; Gintis, Smith, & Bowles., 2001; Henrich, 2004), the distribution of prosocial behaviors in other primate species (reviewed by Silk, 2009), and the ontogeny of prosocial behaviors in human children (Benenson, Pascoe, & Radmore, 2007; Brownell, Svetlova, & Nichols, 2009; Fehr, Bernhard, & Rockenbach, 2008; Moore, 2009; Thompson, Barresi, & Moore, 1997) continues to grow. Some have argued that related traits, potentially including empathy or moral sentiments, can be found among chimpanzees, our closest living primate relatives, and that we inherited these traits from our most recent common ancestor (de Waal, 1997a, 2009). Others have emphasized the fact that altruism is much more limited in chimpanzees than in humans, and argue that the evolution of prosocial preferences is linked to derived human traits, including the capacities that give rise to cumulative cultural evolution (Henrich, 2004) and group-level cooperation (Silk et al., 2005; Burkart, Fehr, Efferson, & van Schaik, 2007), in humans, but not our closest primate relatives. If human prosocial behavior is based on ancestral traits, then we would expect there to be continuities in the prosocial behavior of humans and other primates, particularly other closely related primates such as great apes. If our prosocial behavior is an emergent property of derived traits, then human prosociality should differ markedly from that of chimpanzees.

The current study compares the behavior of children to the behavior of chimpanzees in prior experimental work that is methodologically similar (Silk et al., 2005; Jensen, Hare, Call, & Tomasello, 2006; Vonk et al., 2008; Brosnan et al., 2009; Yamamoto & Tanaka, 2010). The goal is to document the ontogeny of human prosocial behavior within a particular task context that has also been used with nonhuman primates. These tasks are by no means the only way to study prosocial behavior in either humans or chimpanzees, but focusing on a single task enhances our ability to make comparisons across populations. We briefly discuss some of the other relevant work on prosocial behavior in these populations, the methodological differences between them, and how the current study's methods bridge these gaps.

Many studies have found that chimpanzees engage in cooperative behavior such as patrolling territorial boundaries and attacking neighboring groups (Watts & Mitani, 2001), hunting small prey collaboratively (Boesch & Boesch, 1989) and sharing meat and other foods (Nishida & Turner, 1996; Mitani & Watts, 2001; Gilby, 2006), exchanging grooming for other valuable resources (de Waal, 1997b; Mitani, 2006, 2009), and cooperatively guarding mates (Watts, 1998). These and many other findings clearly show that chimpanzees engage in behavior that confers benefits on others. Unfortunately, these behaviors and the methods used to investigate them often cannot clearly be extended for use with humans, so it is difficult to use these data to make direct comparisons between humans and chimpanzees.

Another way to make comparisons between humans and chimpanzees is by using methods based on the logic of experimental research in behavioral economics: subjects are presented with choices that have different material payoffs, and the choices that subjects make reveal their underlying preferences. One advantage of these methods is that they allow costs and benefits to be clearly defined. Another benefit is that they make it possible to present many different populations with the same kinds of choices, permitting direct comparisons between species in a uniform context. For example, Silk et al. (2005) gave one chimpanzee (the actor) the opportunity to choose between two options. One option delivered a food reward to the actor and an identical reward to a group member (the 1/1 distribution). The other option delivered one reward to the actor, but nothing to the other chimpanzee (the 1/0 distribution). The choice between these two payoff distributions is referred to as the Prosocial Game hereafter. Of course, actors might have preferred the 1/1 distribution over the 1/0 distribution because the total number of rewards was greater. So, as a control, actors were also presented with the same set of choices when no recipient was present. If individuals had preferences for outcomes that would benefit others, actors were expected to choose the 1/1 distribution more when a recipient was present than when no recipient was present. Note that prosocial preferences did not compete with self-interest in this task because the actor received the same reward no matter which distribution was chosen. None of the 18 chimpanzees from two different captive facilities displayed behavior that suggested the presence of prosocial preferences (Silk et al., 2005). These results were replicated in the same populations using a slightly different protocol by Vonk et al. (2008) and in different populations by Jensen et al. (2006) and Yamamoto and Tanaka (2010). Similarly, in an experiment in which chimpanzee actors could propose a division of rewards and a recipient could either accept or not accept this proposal (a version of the Ultimatum Game), actors did not tend to make fair proposals, and recipients did not consistently reject unfair proposals (Jensen, Call, & Tomasello, 2007). Thus, in these experimental settings, chimpanzees seem to be indifferent to the outcomes experienced by others.

Much developmental research suggests that even quite young children behave prosocially, but these studies use a plethora of methods. This greatly complicates comparisons among studies of children and between studies of children and chimpanzees. By 1 to 2 years of age, children are responsive to the distress of parents and strangers, both when the distress occurs naturally and when it is caused by the children themselves (Zahn-Waxler & Radke-Yarrow, 1990; Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992). By the end of their second year, children help others, share, provide physical comfort, provide verbal sympathy, protect, and defend victims in distress (Zahn-Waxler & Radke-Yarrow, 1990). Hay, Castle, Davies, Demetriou, and Stimson (1999) found that, under naturalistic observation conditions, 18–30-month-old children shared, and Birch and Billman (1986) also observed sharing among children aged 3–5 when one child received 20 food items for a "special snack" while a second child received only two. Most children shared only small amounts and did so only at the request of their partner. Boys tended to share smaller amounts than girls.

Eisenberg and Fabes (1998) report a meta-analysis of age and sex effects across 125 studies of prosocial behavior in children. They found that prosocial behavior was positively correlated with age and that females were generally more prosocial than males. The age and sex effects differed across three categories of prosocial behavior: instrumental helping, comforting, and sharing/donating (Eisenberg & Fabes, 1998). Most of these studies used methods based on naturalistic observations or reports of behavior by children, parents, or teachers. Eisenberg and Fabes (1998) found significant variation in results across studies using different methods, and this variability could be due to the susceptibility of these methods to experimenter bias (Eisenberg & Fabes, 1998). Most of the studies evaluated by Eisenberg and Fabes (1998) are difficult to compare to those with chimpanzees because of the substantial differences in methodologies used. Further, these developmental findings can give us no clear insight into the *preferences* underlying children's prosocial behavior. Prosocial behavior could be proximally motivated by a desire for future reciprocity or by a concern for the welfare of partners that is not related to one's own payoffs.

Other developmental studies have investigated children's preferences for outcomes that benefit others in ways that avoid some of these methodological differences (Table 1). Several of these studies also indicate that children become more prosocial with age (Harbaugh, Krause, & Liday, 2003; Takezawa, Gummerum, & Keller, 2006; Benenson et al., 2007; Fehr et al., 2008; Brownell et al., 2009; Gummerum, Hanoch, Keller, Parsons, & Hummel, 2009; Blake & Rand, 2010), and all suggest that children behave more prosocially than chimpanzees. However, these studies also differ from the chimpanzee studies in a number of potentially important ways (Table 1). First, studies differed in the discreteness of the choice, with some studies requiring children to make binary choices between reward distributions and others allowing them to allocate any or all of an endowed amount to another player. Second, studies differed in whether food or

Table 1
Design features of the current experiment, and previous experiments with children

Study	Choice was discrete	Reward	Age of recipient	Relationship of Recipient	Recipient present at testing	Participants anonymous	Prosocial outcome delayed	Age (in years)
Chimpanzee studies	Yes	Food	n/a	Social group member	Yes	No	No	n/a
Current experiment	Yes	Food	Child	Schoolmate	Yes	No	No	3–8
Brownell et al. (2009)	Yes	Food	Adult	Unfamiliar	Yes	No	No	1.5–2
Thompson et al. (1997)	Yes	Stickers	Adult	Unfamiliar	Yes	No	No	3–5
Fehr et al. (2008)	Yes	Food	Child	Schoolmate or unfamiliar	No	Yes	Yes	3–8
Moore (2009)	Yes	Stickers	Child	Friend, nonfriend, or unfamiliar	No	No	Yes	4.5–6
Blake and Rand (2010)	No	Stickers	Child	Unfamiliar	No	Yes	Yes	3–6
Benenson et al. (2007)	No	Stickers	Child	Schoolmate	No	Yes	Yes	4–9
Gummerum et al. (2009)	No	Stickers	Child	No data	No	Yes	Yes	3–5
Lucas et al. (2008)	No	Stickers	Adult	Unfamiliar	No	Yes	Yes	4
Murnighan and Saxon (1998), experiment 1	No	Money and food	Child	Schoolmate	Yes	No	No	5–11
Sally and Hill (2006)	No	Stickers	Child	No data	No	Yes	Yes	6–10
Harbaugh and Krause (2000)	No	Toys/school supplies	Child	Schoolmate	No	Yes	Yes	6–12
Leman et al. (2009)	No	Money	Child	No data	No	Yes	Yes	7–17
Harbaugh et al. (2003)	No	Money	Child	Schoolmate	No	Yes	Yes	7–18
Harbaugh et al. (2007)	No	Toys/school supplies	Child	Schoolmate	No	Yes	Yes	8–18
Gummerum et al. (2008)	No	Money	Child	Unfamiliar	No	Yes	Yes	8–16
Almas et al. (2010)	No	Money	Child	Possibly unfamiliar or schoolmate	No	Yes	Yes	10–18
Takezawa et al. (2006)	No	Money	Child	Unfamiliar	No	Yes	Yes	11–14

nonfood payoffs (e.g., stickers) were used, a potentially significant difference because existing work suggests that chimpanzees may respond differently to food and nonfood rewards (Boysen & Berntson, 1995; Boysen, Berntson, Hannan, & Cacioppo, 1996). Third, in some studies, the delivery of rewards was delayed, rather than immediate. Finally, and perhaps most importantly, relationships between partners also differ across studies. In some cases, children's partners were unfamiliar adults; in others, they were known individuals who were not physically present or unknown individuals who were not physically present.

These procedural differences make it difficult to compare the performance of chimpanzees and children directly in these tasks and to identify how and at what age children's behavior is clearly discriminable from that of chimpanzees. This gap in our ability to directly compare the behavior of human children and chimpanzees is the focus of the current study, and to address this issue, our experiment was designed to replicate the protocol of previous chimpanzee studies of prosocial preferences as closely as possible. Here, children were paired with familiar peers in a face-to-face setting and manipulated an apparatus that was very similar to one of the apparatuses used in previous work with chimpanzees (Silk et al., 2005). Actors were presented with a set of binary choices between options with different distributions of food rewards (adapted from Silk et al., 2005 and Fehr et al., 2008), which were delivered immediately. In the Prosocial Game, actors were offered a choice between 1/1 and 1/0 distributions. In the Costly Sharing Game, actors were offered a choice between 1/1 and 2/0 distributions. In this case, actors incur a cost when they deliver rewards to others. In the Envy Game, actors were offered a choice between 1/1 and 1/2 distributions. In this case, the actor can choose an equitable distribution or an inequitable distribution that advantages the recipient. We included a control condition in which no recipient children were present to receive rewards, which served as the baseline for comparisons in our primary analyses. We compared children's behavior when they played the games face-to-face with a peer recipient (the "present" condition) to their behavior in the control condition where they played the games without a recipient (the "absent" condition). As illustrated in Table 1, these methodological features allow direct comparisons between our own results and those of previous studies of prosocial behavior in chimpanzees and human children.

2. Methods

2.1. Participants

We included in our analyses 92 children (37 female; 55 male) between the ages of 3 and 8 years, as follows: ages 3–4: N=27, mean age=4.33, S.D.=.43; ages 5–6: N=38, mean age=5.92, S.D.=.64; and ages 7–8: N=27, mean age=7.69, S.D.=.42. Six participants were excluded from the analysis due to experimenter error (N=2), equipment error (N=3), or inattention by the participant (N=1).

Children sometimes played the roles of both actor and recipient in separate sessions. However, children always played the role of actor first and recipient second. No child ever had any first-hand experience with the task before participating as an actor, and children were not told that they would next play the game as a recipient except in a minority of cases in which the child specifically asked if they would play a second time.

Participants were recruited at preschools and elementary schools in the Los Angeles area. Letters and consent forms were distributed to parents by the experimenter as the children and parents arrived for school in the morning (or left for the day in the afternoon) or through weekly homework packages distributed to parents by the teachers.

2.2. Task

The apparatus was adapted from Silk et al. (2005). The apparatus consisted of a platform (24″ long by 24″ wide) that anchored two mechanisms and the ropes used to operate them (Fig. 1). A child (the actor) could pull these ropes to deliver transparent cups containing payoffs (normally Goldfish brand cheddar cheese crackers; occasionally raisins for children with allergies) to themselves and another child (the recipient). Each mechanism distributed a particular set of payoffs to the actor and recipient, while simultaneously retracting the handle for the alternate mechanism. Thus, by choosing to operate one mechanism and access its payoffs, the actor forfeited the payoffs associated with the alternate mechanism.

The payoff distributions were adapted from previous studies on chimpanzees and children. The two mechanisms could be loaded so that they delivered different distributions (Table 2). Each pair of payoffs defines a "game," and the actor's payoff is always listed first in the pair. There were three games: Prosocial (1/1 vs. 1/0), Envy (1/1 vs. 1/2), and Costly Sharing (1/1 vs. 2/0). In the Prosocial Game, actors could confer benefits on recipients at no cost to themselves. The Envy Game allowed actors to deliver payoffs to recipients that matched their own payoff or were greater than their own payoff. In the Costly Sharing Game, actors incurred a cost when they conferred benefits on recipients.

2.3. Procedure

The experiment took place at preschools and elementary schools in Los Angeles during the school day. Teachers and other children were often within sight, but rarely watched or were close to the testing area. Children were seated either on the ground or at a child-sized table, and a video camera recorded their choices. Each experimental session consisted of a training phase and a test phase, with the entire session lasting about 10 min. When the session was concluded, the recipient returned to class, and the actor became the recipient

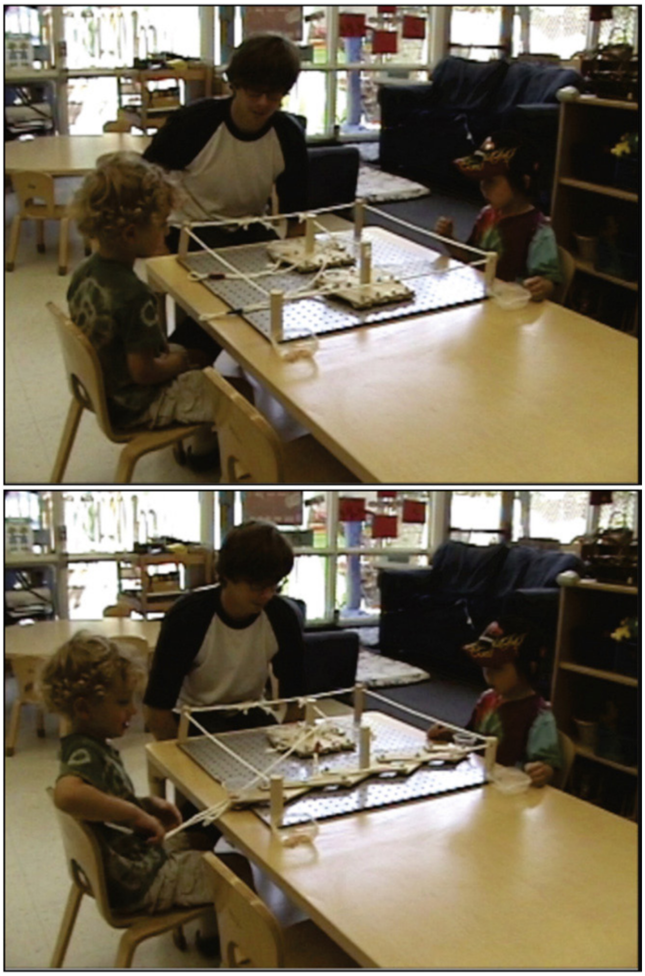

Fig. 1. Experimental apparatus.

for the next session. A new actor was brought in, and the procedure was repeated.

2.4. Training

Each actor received a minimum of four training trials, during which recipients were also present. The experimenter first showed the actor how to operate the mechanisms and then explained the rules of the "game" to both participants: (a) they could only take rewards that were delivered to them when the cup moved past the boundary rope that encircled the apparatus; (b) they could not reach in and retrieve rewards from beyond the rope; and (c) for each trial, the actors could choose whichever mechanism they wanted, but they could not choose both.

For training trial #1, one mechanism was loaded with a 1/1 payoff (the other mechanism was left empty), and the actor was allowed to pull a handle. For training trial #2, the alternate mechanism was loaded with a 1/0 payoff (the mechanism used in trial #1 was left empty). Training trials #3 and #4 were the same as training trials #1 and #2 (respectively). Side of presentation was counterbalanced, with training trial #1 sometimes using the left mechanism (N=40) and sometimes using the right mechanism (N=52). After the actor made a choice on each training trial, the experimenter asked both actor and recipient if they received anything. This highlighted for the actor that the recipient sometimes received a payoff, but did not in all cases.

The experimenter's verbal responses were the same across all trials, and no feedback on children's performance was given. If on any training trial the actor chose the empty mechanism that delivered no rewards, the trial was completed and immediately repeated. Only one child chose the empty mechanism repeatedly; this session was aborted and excluded from analysis because the child was inattentive.

2.5. Test

Following the training phase, actors were presented with six test trials. These were divided into two conditions of three trials each. The two counterbalanced conditions were "present" (in which the recipient was present and received payoffs) and "absent" (in which there was no recipient). The three trials in each condition corresponded to each of the three games: Prosocial, Envy, and Costly Sharing. Thus, children each got one trial with each game in each of the two conditions. The order of the three games was counter-balanced within conditions, but fixed across conditions.

During the test phase, the position of the 1/1 distribution (i.e., whether it was loaded in the left or right mechanism) alternated on successive trials. The starting position of the 1/1 distribution was always on the left mechanism.

It was important that the children understood that choosing one mechanism and payoff distribution forfeited the alternative distribution and that no one (not even the experimenter) received the other set of payoffs. Thus, at the end of every test trial, the experimenter made a point of showing the actor the unselected payoffs and placing them in a garbage can while saying, "And, these ones go in the trash!"

2.6. Coding

Choices of the 1/1 distribution were assigned a value of 1, and choices of the other distributions (1/0, 2/0, and 1/2) were assigned a value 0. Children's choices were coded online and recoded offline using video recordings by a coder who was naïve to the age of the participants.

Children's affective behavior during each experimental trial was also coded from the videotape, specifically whether or not the actor laughed out loud at any point

Table 2
Payoff distributions of games in the current study

Game	Payoff #1	Payoff #2
Prosocial Game	1/1	1/0
Costly Sharing Game	1/1	2/0
Envy Game	1/1	1/2

within each trial. A second naïve rater coded 44 out of 92 total sessions, and interrater agreement was substantial (Cohen's kappa=0.75).

We also coded expressions of desire for a reward similar to the ones used by Brownell et al. (2009) and requests made by recipients for specific distributions. No explicit expressions of desire were observed by either rater. Interrater reliability for whether or not a recipient requested a specific payoff was high (Cohen's kappa=.90).

2.7. Analyses

In each game, subjects made binary choices between two options in two conditions (present/absent). These choices were analyzed in two ways. The primary analyses compared children's choices in each game across the two conditions, as was done by Silk et al. (2005) and Brownell et al. (2009). Note that this comparison between conditions removes the need to compare children's choices to chance. This is especially useful because it is not clear that "chance" behavior would mean the same thing in the Costly Sharing Game as it does in the Prosocial and Envy Games. The secondary analyses examined how patterns of choice across the three games differed as a function of age following Fehr et al. (2008).

For the primary analyses, we used multilevel logistic regression models (with "child ID" as a random effect) to assess the factors that predicted whether or not children chose the 1/1 distribution. *Condition* (whether or not a recipient was present) is our most theoretically important variable. This variable indicates whether or not children choose 1/1 more frequently when a recipient was present than when no recipient was present. In the Prosocial and Costly Sharing Games, 1/1 is both the most prosocial and egalitarian outcome. In the Envy Game, 1/1 is the most egalitarian outcome, but it is also the *less* prosocial outcome. *Condition* is thus our fundamental metric of prosocial behavior. If children's choices of 1/1 are systematically influenced by the presence of a recipient, then the regression coefficients of this variable across these three games should indicate whether children are prosocial or egalitarian. A positive coefficient for *Condition* in the Prosocial and Costly Sharing Games indicates that children are more prosocial or egalitarian. However, in the Envy Game, a negative coefficient indicates greater prosociality, while a positive coefficient may indicate greater egalitarianism.

The results of the meta-analysis reported by Eisenberg & Fabes (1998) and many other previous studies of prosocial behavior in children led us to hypothesize that both age and sex might predict children's behavior in this experiment, but we had no a priori predictions about many other variables which could influence children's responses. To evaluate how well different factors explained our data, we created models containing all possible combinations of these factors and identified how well each of these models fit the data. The factors that appeared often in the models that best fit the data are likely to be most important for understanding children's behavior in these games. This procedure provides information about how robust effects are to changes in model structure. It gives us insight into how important particular factors are, above and beyond the regression coefficients associated with particular factors in particular models. The procedure is not biased by our a priori predictions about which factors would be important and thus diminishes concerns that our results are biased by our predictions. This is important because the variable *Laughter* (whether or not actor laughed during the trial) was not predicted a priori but emerged as a variable of interest during the course of the study. We will discuss the influence and significance of laughter in greater detail below.

In total, we considered 12 factors in addition to *Condition*: three categorical, three continuous, and six interaction terms. Categorical variables were *Laughter*, *Siblings*, and *Sex of Actor*. *Laughter* and *Siblings* were coded such that 1=yes (i.e., actor did laugh, actor had at least one sibling) and 0=no. Sex was coded so that 1=female and 0=male. Continuous variables were *Age of Actor, Birth Order* (of actor), and *Trial* (trial number). Interaction terms were *Condition* × *Sex*, *Condition* × *Siblings*, *Condition* × *Birth Order*, *Condition* × *Age*, *Condition* × *Laughter*, and *Age* × *Laughter*.

These 13 variables yield 8192 possible combinations of factors, which were used to create 8192 different models. We then independently tested the data obtained from each game against each of these models and evaluated the goodness of fit of each of these models using Akaike weights (Burnham & Anderson, 2002; McElreath et al., 2008). Akaike weights for each model are calculated using that model's Akaike Information Criterion (AIC; Akaike, 1973). AIC values trade off the goodness of fit for a particular model with the number of parameters that model includes, such that, for a given set of models, the models with the lowest AIC are interpreted as the models that best fit the data using the fewest number of parameters. This is a conservative approach that penalizes overfitting models to data. Akaike weights can be interpreted as probabilities: a model's Akaike weight represents the probability that this model is the best model out of all models being considered. Summing the Akaike weights for all models that include a particular factor (e.g., *Age*) generates the probability that the best model includes this factor. These probabilities were calculated for each factor independently for each game (Prosocial Game: Table 3a, Costly Sharing Game: Table 3b, Envy Game: Table 3c), and each probability reflects the likelihood that a factor is important for understanding our data. We then create models using each of these factors (Tables 4a–c), which allow us to test how these factors predict children's choice of 1/1 outcomes.

2.8. Patterns of choice

For the secondary set of analyses, we coded children's pattern of choices across the three games according to the

Table 3a
Models for the Prosocial Game

DV: choice of 1/1 outcome	Probability that the best model includes this factor	Models												
		1	2	3	4	5	6	7	8	9	10	11	12	13
		Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)
Condition	.45	.35 (.297)							−.12 (.931)	.51 (.386)	.72 (.703)	.82 (.698)	.69 (.328)	.70 (.330)
Trial	.52		−.12 (.088)											
Age of Actor	.46			−.23 (.109)					−.27 (.134)					−.14 (.116)
Sex of Actor	.27				.07 (.302)					.27 (.426)				
Siblings	.84					.50 (.383)					.74 (.558)			
Birth Order	.31						.16 (.196)					.30 (.280)		
Laughter	.99							−.47 (.419)					.77 (.740)	14.23 (5.93)
Condition × Age of Actor	.46								.08 (.151)					
Condition × Sex of Actor	.27									−.40 (.606)				
Condition × Siblings	.36										−.45 (.776)			
Condition × Birth Order	.33											−.29 (.394)		
Condition × Laughter	.97												−2.07 (.926)	−4.22 (1.78)
Age × Laughter	.98													−2.09 (.888)
Random effect (child ID)		.004 (.041)	.004 (.040)	.003 (.034)	<.001 (.016)	.003 (.025)	.002 (.367)	.002 (.369)	.002 (.307)	.004 (.042)	.004 (.039)	.004 (.041)	.003 (.030)	.002 (.327)
Constant		<−.001	.61	1.53	.15	−.24	−.08	.24	1.60	−.11	−.61	−.48	−.07	.78

The probability that each factor appears in the best model (out of all 8192 models considered) is calculated by summing the Akaike weights for all models that include that factor. Factors with probabilities close to 1 are the factors most likely to explain the data well, irrespective of exact model structure. Each model provides regression coefficients and standard errors for each factor that has been included in the model. Standard errors can be used to calculate 95% confidence intervals (coefficient±1.96∗standard error), and if the coefficient is greater than 1.96 times the standard error, this suggests that the estimate is different from zero. The last row provides the variance estimate for the random effect for each model. These estimates are all small and are smaller than their standard errors, suggesting that there is little variation between children in how they play this game.

Table 3b
Models for the Costly Sharing Game

DV: choice of 1/1 outcome	Probability that the best model includes this factor	Models												
		1	2	3	4	5	6	7	8	9	10	11	12	13
		Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)
Condition	.35	1.04 (.475)							−.90 (.1.67)	.21 (.648)	−.35 (.847)	−.24 (1.17)	1.24 (.502)	1.20 (.503)
Trial	.93		−.38 (.147)											
Age of Actor	.98			−.54 (.192)					−85 (.341)					−.50 (.216)
Sex of Actor	.44				1.14 (.490)					.26 (.783)				
Siblings	.77					−1.17 (.558)					−2.49 (.936)			
Birth Order	.49						−.40 (.344)					−1.07 (.721)		
Laughter	.32							−.59 (.654)					−.24 (1.31)	2.69 (3.78)
Condition × Age of Actor	.32								.37 (.316)					
Condition × Sex of Actor	.79									1.71 (.985)				
Condition × Siblings	.62										2.05 (1.07)			
Condition × Birth Order	.36											.89 (.784)		
Condition × Laughter	.40												−.91 (1.49)	−.74 (1.52)
Age × Laughter	.32													−.49 (.655)
Random effect (child ID)		1.32 (.577)	1.23 (.578)	.84 (.590)	.93 (.570)	.90 (.565)	1.04 (.549)	1.05 (.547)	1.11 (.607)	1.35 (.621)	1.31 (.617)	1.27 (.582)	1.22 (.572)	1.04 (.588)
Constant		−2.57	−.73	1.35	−2.31	−.88	−1.20	−1.74	2.26	−2.70	−.81	−.98	−2.47	.47

The probability that each factor appears in the best model (out of all 8192 models considered) is calculated by summing the Akaike weights for all models that include that factor. Factors with probabilities close to 1 are the factors most likely to explain the data well, irrespective of exact model structure. Each model provides regression coefficients and standard errors for each factor that has been included in the model. Standard errors can be used to calculate 95% confidence intervals (coefficient±1.96∗standard error), and if the coefficient is greater than 1.96 times the standard error, this suggests that the estimate is different from zero. The last row provides the estimate for the random effect parameter for each model. These estimates are all larger than the estimates for models in the Prosocial and Envy Games, and are large relative to their standard errors, suggesting that there is relatively more variation between children in how they play this game.

Table 3c
Models for the Envy Game

DV: choice of 1/1 outcome	Probability that the best model includes this factor	Models												
		1	2	3	4	5	6	7	8	9	10	11	12	13
		Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)	Coef. (S.E.)
Condition	.38	∼.00 (.296)							−.68 (.947)	.22 (.383)	−1.21 (.718)	−.73 (.695)	−.16 (.317)	−.18 (.318)
Trial	.36		−.09 (.087)											
Age of Actor	.33			.12 (.107)					.07 (.131)					.04 (.116)
Sex of Actor	.27				−.04 (.301)					.24 (.428)				
Siblings	.56					.16 (.380)					−.58 (.558)			
Birth Order	.29						.01 (.193)					−.21 (.274)		
Laughter	.49							.51 (.446)					−.09 (1.01)	−5.09 (2.95)
Condition × Age of Actor	.30								.12 (.155)					
Condition × Sex of Actor	.36									−.55 (.604)				
Condition × Siblings	.30										1.48 (.789)			
Condition × Birth Order	.41											.45 (.392)		
Condition × Laughter	.35												.81 (1.13)	1.35 (1.27)
Age × Laughter	.56													.70 (.395)
Random effect (child ID)		<.001 (.011)	<.001 (.012)	<.001 (.011)	<.001 (.011)	<.001 (.011)	<.001 (.011)	<.001 (.086)	<.001 (.081)	<.001 (.012)	.002 (.323)	<.001 (.086)	.002 (.305)	.001 (.178)
Constant		.13	.44	−.61	.15	∼.00	.11	.06	−.27	.04	.61	.47	.13	−.07

The probability that each factor appears in the best model (out of all 8192 models considered) is calculated by summing the Akaike weights for all models that include that factor. Factors with probabilities close to 1 are the factors most likely to explain the data well, irrespective of exact model structure. Each model provides regression coefficients and standard errors for each factor that has been included in the model. Standard errors can be used to calculate 95% confidence intervals (coefficient±1.96∗standard error), and if the coefficient is greater than 1.96 times the standard error, this suggests that the estimate is different from zero. The last row provides the variance estimate for the random effect for each model. These estimates are all small and are smaller than their standard errors, suggesting that there is little variation between children in how they play this game.

Table 4
Coding schemes for patterns of choice across the three games (Fehr et al., 2008)

Pattern of choice	Choice in Prosocial Game	Choice in Costly Sharing Game	Choice in Envy Game
Strongly egalitarian	1/1	1/1	1/1
Weakly egalitarian	1/1	2/0	1/1
Strongly generous	1/1	1/1	1/2
Weakly generous	1/1	2/0	1/2
Spiteful[a]	1/0	2/0	1/1

[a] Spite here is “weak” because it is not costly for the actor to reduce the recipient’s payoff.

eight categories used by Fehr et al. (2008): strongly egalitarian, weakly egalitarian, strongly generous (i.e., strongly prosocial), weakly generous, spiteful, and three ambiguous patterns (Table 4). We then tested whether the frequencies of each of these eight patterns exceeded what would be expected by chance using a two-tailed binomial test.

3. Results

3.1. Prosocial Game (1/1 vs. 1/0)

Overall, a larger proportion of children chose 1/1 when the recipient was present (proportion of trials=0.59, N=92) than when the recipient was absent (proportion=0.50, N=92). In Model 1 (Table 3a), *Condition* (i.e., recipient’s presence) has a positive coefficient (suggesting that children were more likely to choose 1/1 in the recipient-present condition), but this effect is weak. Further analyses indicate that this effect is suppressed by a factor that we did not anticipate. A number of children laughed aloud when they made their choices, and children were more likely to laugh when another child was present during the trial (proportion of trials=0.24, N=92) than when the recipient was absent (proportion=0.08, N=92).

The probability with which the best model includes *Condition* is low, suggesting that a main effect of *Condition* is not very informative for interpreting children’s behavior in this game. *Condition* does appear with substantial coefficients and small standard errors in Models 12 and 13 (Table 3a), but this suggests that *Condition* only does a good job of predicting children’s choices of 1/1 in those models that include *Condition* × *Laughter*. The negative coefficient for this interaction in Models 12 and 13 indicates that children chose 1/1 substantially *less* on trials in which they laughed in the present condition than when they did not laugh or when they were in the absent condition. The main effect of *Condition* only becomes substantial when this *Condition* × *Laughter* interaction is controlled (Models 12 and 13). Thus, children appear to be prosocial overall, but only after controlling for the nonprosocial tendencies of children who laugh (Fig. 2). The probability that the best model includes *Condition* × *Laughter* is near 1, and this means that the interaction of *Condition* and *Laughter* is much more informative for predicting children’s behavior than is a main effect of *Condition*.

In Models 7 and 12 (Table 3a), *Laughter* does not have a strong predictive effect on children’s behavior. However, the probability that *Laughter* appears in the best model is very

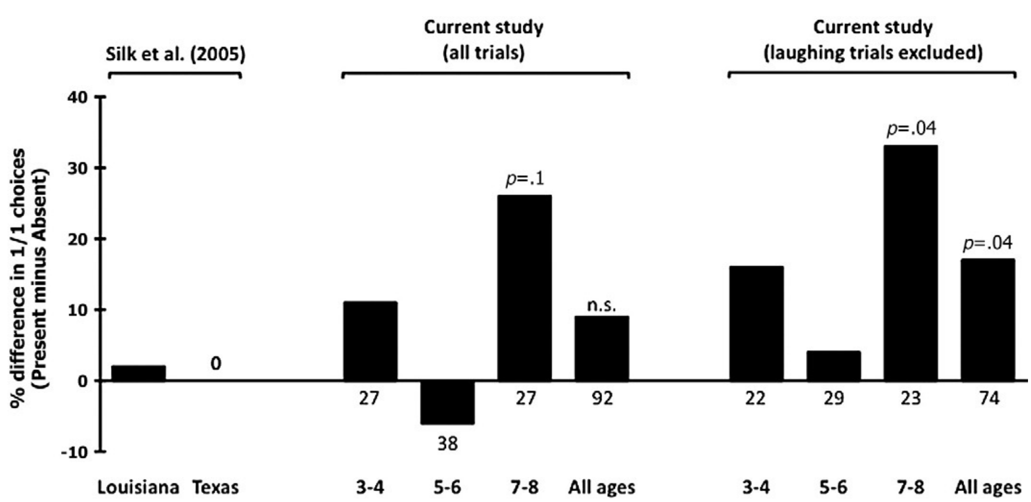

Fig. 2. Choices of 1/1 in the Prosocial Game, presented as the percentage of 1/1 choices in the present condition minus percentage of 1/1 choices in the absent condition. This difference directly represents whether children tended to choose 1/1 more frequently in the present condition than in the absent condition, which is our primary measure of prosocial behavior. Also, since the same subjects contribute to both conditions, subtracting them removes noise in the subjects’ behavior that is irrelevant to this primary measure. Positive deflections of columns in the figure below represent prosocial tendencies, negative deflections represent antisocial tendencies, and the absence of deflection (a value of zero) represents either indifference or ambivalence on the part of actors towards the outcomes received by recipients. Chimpanzees’ choices (Silk et al., 2005) are plotted, along with children’s choices in the current study. Children’s choices are plotted both including all trials and also excluding trials during which the actor laughed. Differences in % between the two conditions are on the vertical axis, while populations of chimpanzees and age groups of children (e.g., 3–4 years) are on the horizontal axis. Values below each bar correspond to the number of participants in that group. The p values describe the difference between choices of 1/1 in the two conditions (Fisher’s Exact Tests).

high, and in Model 14, the large positive coefficient for *Laughter* suggests that children showed a strong main effect of choosing 1/1 more when they laughed. *Age* × *Laughter* is also very likely to be in the best model, and the negative coefficient for this interaction in Model 13 indicates that the main effect of *Laughter* is mainly driven by the behavior of young children. Older children were substantially less likely to choose 1/1 on trials in which they laughed than in trials in which younger children laughed or trials in which there was no laughing. The large positive coefficient for *Laughter* only appears after controlling for the significant negative effect of *Age* × *Laughter* (Model 13), which indicates that the overall effect of children choosing 1/1 more when they laugh mainly reflects the behavior of younger children. We discuss the significance of laughter in more detail in the discussion.

Models 3 and 8 (Table 3a) suggest a strong effect of *Age of Actor*, with older children being overall less likely than younger children to choose 1/1. However, the relatively low probability that *Age of Actor* appears in the best model suggests that this effect is not very important for understanding children's behavior, and this is confirmed by the fact that the main effect of *Age of Actor* is reduced when *Age* × *Laughter* is included in Model 13. This implies that the overall main effect of *Age of Actor* is driven mainly by a developmental increase in children's tendency to choose 1/0 when they laugh (i.e., an increase in the main effect of *Laughter*) and explains why *Age of Actor* has a relatively low probability of being included in the best model.

Siblings has a relatively high probability of being included in the best model, and in both Models 5 and 10 (Table 3a), the coefficient for this factor is positive, suggesting that children generally chose 1/1 more frequently when they had siblings. However, the coefficients and standard errors for this factor suggest that the main effect of having siblings is not very strong. Model 10 also gives no reason to think that children with siblings are more or less prosocial than only children since the interaction of *Condition* and *Siblings* has small coefficients, has large standard errors, and is unlikely to be included in the best model. None of the other factors considered have high probabilities of being included in the best model, and none appear to influence the effect of *Condition* nor show much evidence of independently predicting children's choices of 1/1.

3.2. Costly Sharing Game (1/1 vs. 2/0)

Across both conditions, children were two thirds less likely to choose the 1/1 option on trials in the Costly Sharing Game (proportion of trials=0.18, *N*=184) than in the Prosocial Game (proportion=0.54, *N*=184), and this presumably reflects the elevated cost of the prosocial option in the Costly Sharing Game. However, children were twice as likely to choose the 1/1 distribution when the recipient was present during the trial (proportion of trials=0.24, *N*=92) as when the recipient was absent (proportion=0.12, *N*=92). This was reflected in the substantial main effect of *Condition* observed in Model 1 (Table 3b), which suggests that children were prosocial in this game. However, the probability that the best model included *Condition* was low, and further analyses suggest that this main effect is best explained through interactions with other factors.

Females were substantially more prosocial in the Costly Sharing Game than were males, as illustrated in Fig. 3. This is reflected in the strong positive coefficient for the interaction between *Condition* and *Sex of Actor* in Model 4 (Table 3b). This variable indicates that females chose 1/1 substantially more on trials in the present condition relative to males in the present condition and children of both sexes in the absent condition. As with *Condition*, the probability that the best model includes *Sex of Actor* is low, and when *Condition* × *Sex of Actor* is included in Model 9 (Table 3b), the main effects of *Condition* and *Sex of Actor* are both dramatically reduced. The implication of this is that females are solely responsible for the main effect of *Condition* from Model 1 (Fig. 3).

Trial and *Age* both have a high probability of being included in the best model. In Model 2, *Trial* negatively predicts children's choices of 1/1, meaning that children chose 2/0 more frequently as the experiment progressed (Table 3b). Model 8 shows that *Age* also positively predicts children's 2/0 choices: older children were more willing to choose the self-maximizing outcome (Table 3b). *Siblings* also has a relatively high probability of being in the best model, and Models 5 and 10 both indicate that actors with siblings chose 2/0 more than

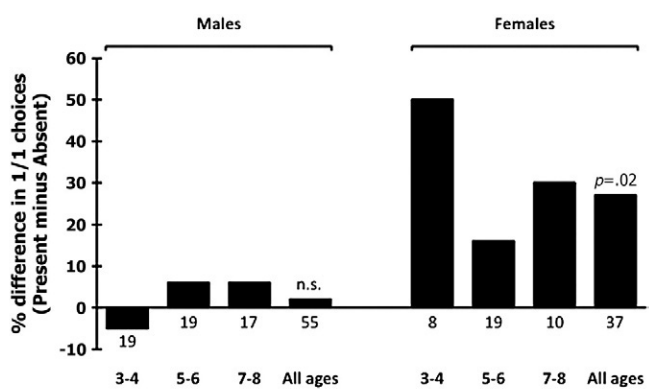

Fig. 3. Choices of 1/1 in the Costly Sharing Game, presented as percentage of 1/1 choices in the present condition minus percentage of 1/1 choices in the absent condition. This difference directly represents whether children tended to choose 1/1 more frequently in the present condition than in the absent condition, which is our primary measure of prosocial behavior. Also, since the same subjects contribute to both conditions, subtracting them removes noise in the subjects' behavior that is irrelevant to this primary measure. Positive deflections of columns in the figure below represent prosocial tendencies, negative deflections represent antisocial tendencies, and the absence of deflection (a value of zero) represents either indifference or ambivalence on the part of actors towards the outcomes received by recipients. Both males' choices and females' choices are plotted. Differences in % between the two conditions are on the vertical axis, while age groups (e.g., 3–4 years) are on the horizontal axis. Values below each bar correspond to the number of participants in that group. The *p* values describe the difference between choices of 1/1 in the two conditions (Fisher's Exact Test).

did actors who were only children (Table 3b). There is also evidence that *Siblings* interacts with *Condition* and that children with siblings are more prosocial than only children. In Model 10, *Condition* × *Siblings* appears with a substantial positive coefficient, suggesting that only children are less likely to choose 1/1 more frequently in the present condition than in the absent condition. This is despite the fact that, overall, only children choose 1/1 more frequently. However, the probability that the best model includes *Condition* × *Siblings* is not as substantial as that for *Condition* × *Sex,* suggesting that *Condition* ×*Siblings* is relatively less likely to be important for explaining children's behavior in the Costly Sharing Game.

It is also worth noting that although the effect of *Condition* in the Prosocial Game could have been driven by children being averse to wasting food (i.e., they chose 1/1 in the present condition so that less food went in the trash, not because it was prosocial), this cannot explain the effect of *Condition* in the Costly Sharing Game. Here, regardless of whether children choose 1/1 or 2/0, two food items would go in the trash.

3.3. Envy Game (1/1 vs. 1/2)

In this game, 1/1 is the egalitarian option, while 1/2 might be characterized as a more prosocial option because the partner obtains a greater payoff. Across both conditions, children were as likely to choose the 1/1 option on trials in the Envy Game (proportion of trials=0.53, N=184) as they were in the Prosocial Game (proportion=0.54, N=184). Additionally, equal proportions of actors chose the 1/1 distribution in the Envy Game in the present condition (proportion=0.53, N=92) and absent condition (proportion=0.53, N=92).

There is no main effect of *Condition* in Model 1 (Table 3c), and the probability that this factor appears in the best model is low. Indeed, the probabilities for all factors are low, suggesting that they provide less insight into children's behavior in this game than in the other games. However, a somewhat marginal main effect of *Condition* suggests that children did tend to choose 1/2 more in the present condition than in the absent condition, but only in Model 10 (Table 3c) when the interaction between *Condition* and *Siblings* has been controlled. The positive coefficient for this interaction term indicates that children with siblings chose 1/1 more frequently (were more envious) than only children in the present condition and more frequently than all children chose 1/1 in the absent condition. The relatively small standard errors for *Condition* and *Condition* × *Siblings* suggest that children with siblings were more egalitarian than only children, an interpretation which could also be applied to the similar pattern of behavior these children displayed in the Costly Sharing Game (Table 3b). However, the probability that *Condition* × *Siblings* appears in the best model is low, suggesting that these effects may be inconsistent and highly sensitive to model structure. Additionally, our sample included relatively few children without siblings (only 17 children out of 92), so the results for *Siblings* across all games are necessarily tentative.

In Model 13, *Age* × *Laughter* indicates that older children chose 1/1 marginally more frequently when they laughed, relative to younger children and relative to trials in which there was no laughing. The marginal main effect of *Laughter* in Model 13 points in the other direction, with children showing a tendency to choose 1/2 more when the they laughed during a trial. The negative coefficient for *Laughter* means that children were less likely to choose 1/1 when they laughed. In other words, children chose the 1/2 option more often when they laughed, but this effect was reduced among older children. These results are qualitatively very similar to those obtained from the Prosocial Game (Table 3a), but are less consistent across subjects.

3.4. Patterns of choice

We compiled the responses of subjects into five categories, following Fehr et al. (2008). Three additional "ambiguous" categories were not analyzed (Fehr et al., 2008). Table 4 illustrates this categorization scheme, and Fig. 4 presents the results. A larger percentage of children aged 3–4 were weakly generous (i.e., weakly prosocial) than would be expected by chance (41%, two-tailed binomial test: p<.001, N=92). The percentage of children who were weakly generous was halved among 5–6-year-olds (to 21%) and

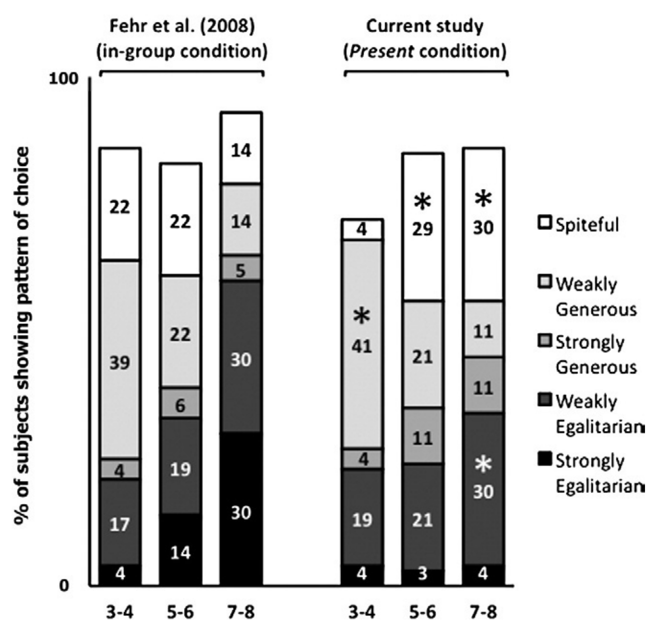

Fig. 4. Percentages of children in each of the three age groups that conform to the five nonambiguous patterns of choice appear for both the present condition of the current study and the in-group condition of Fehr et al. (2008). Ambiguous patterns make up the difference in height between each bar and 100%. Percentages of children showing a pattern are on the vertical axis, while age groups (e.g., 3–4 years) are on the horizontal axis. Asterisks indicate patterns of choice which appear more often than would be expected by chance (p<.05, two-tailed binomial test).

halved again among 7–8-year-olds (to 11%). Spitefulness appeared more often than chance would predict at age 5–6 years (29%, p=.005, N=92) and 7–8 years (30%, p=.01, N=92), percentages seven times larger than among 3–4-year-olds (4%). Weakly egalitarian choice patterns also appeared among 7–8-year-olds more than would be expected by chance (30%, p=.01, N=92), an increase of about 50% over 3–4- and 5–6-year-olds.

3.5. Recipients' expressions of desire and requests for specific payoffs

None of the recipients ever expressed a general desire for a reward, as adult confederates were instructed to do by Brownell et al. (2009). On 12% of all recipient-present trials (N=276), the recipient explicitly requested one of the two distributions. Virtually all of these requests were for the self-maximizing distribution. Recipients made requests on about equal numbers of trials in the Prosocial Game (proportion of trials=0.13, N=92) and Envy Game (proportion=0.16, N=92). In the Costly Sharing Game, children made requests on fewer trials (proportion=0.08, N=92), but this difference was not significant in comparison to either the Prosocial or Envy Game. Actors delivered the requested distribution on only about half these trials (proportion=0.56, N=34), and actors did not choose the prosocial option significantly more often when the recipient made a request.

4. Discussion

Here we will first discuss what our results imply about differences between human children and chimpanzees, and argue that the current study provides the best test currently available for differences between chimpanzees and humans, given the many inconsistencies in methods and results in the literature on prosocial behavior in chimpanzees. We will then discuss how these results relate to past work on the development of prosocial behavior in children. As has been reported by other studies, we observe effects of age and sex in children's prosocial behavior, which we discuss. We also find evidence for an important effect of children's laughter or, perhaps more likely, their sense of humor and developing understanding of normative behavior. Finally, we discuss some observed effects of having siblings and effects of experience with the task (i.e., effects of *Trial*).

The results of this study suggest that even very young children differ from chimpanzees in situations in which they must make choices about the distribution of valued rewards in face-to-face settings. Children were significantly more likely to choose the prosocial option when recipients were present than when recipients were absent in both the Prosocial and Costly Sharing Games. In contrast, chimpanzees did not meet this criterion in the Prosocial Game (Silk et al., 2005; Jensen et al., 2006; Yamamoto & Tanaka, 2010) or in a variant of the Envy Game (0/0 vs. 0/1; Jensen et al., 2006). These findings indicate clear differences between children and chimpanzees, but it is difficult to say with certainty what causes these differences. It is possible that these tasks are more demanding for chimpanzees than they are for even very young children. It is possible that the presence of adult experimenters creates a crucially different social context for children than it does for chimpanzees. Different tasks or experimental contexts may generate different results, as we can see from the fact that differences between children and chimpanzees are more pronounced in experiments in which subjects must make choices between two options (Silk et al., 2005; Jensen et al., 2006; Brosnan et al., 2009; Yamamoto & Tanaka, 2010) than in "instrumental helping" tasks in which subjects are given the opportunity to help others retrieve out-of-reach objects (Warneken & Tomasello, 2006; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Greenberg, Hamann, Warneken, & Tomasello, 2010; Melis et al., 2011).

However, even in instrumental helping tasks, children are substantially more helpful than chimpanzees, and chimpanzees do not show sensitivity to social context in that they provide help at comparable rates to both conspecifics (Warneken et al., 2007) and human experimenters (Warneken & Tomasello, 2006; Warneken et al., 2007). Several instrumental helping studies have found significant differences in helping between test and control conditions in which help is not needed, and concluded that chimpanzees behave prosocially (reviewed by Silk & House, 2011; Warneken & Tomasello, 2009). However, the median rates of helping behavior in these tasks are about 45%, slightly lower than the median rates of helping behavior in the Prosocial Game (Silk & House, 2011). These facts suggest that different tasks and social contexts may not influence chimpanzees' behavior to a very large degree. It will be useful for future work to explicitly explore how experimental tasks and contexts influence prosocial behavior in chimpanzees. This will help to unify the experimental work with captive chimpanzees discussed here and allow this body of work to be integrated with the extensive literature on prosocial and cooperative behavior in wild chimpanzees (Boesch & Boesch, 1989; Nishida, Hasegawa, Hayaki, Takahata, & Uehara, 1992; Watts & Mitani, 2001; Muller & Mitani, 2005; Gilby, 2006; Mitani, 2006).

4.1. Effects of age

Spontaneous prosocial responses in face-to-face versions of the Prosocial Game seem to emerge as children reach 3–4 years of age. At 18 months of age, children do not differentiate between the test and control condition in the Prosocial Game, even when adult recipients verbalize desires for rewards (Brownell et al., 2009). At 25 months of age, children respond to adults' verbalizations of desire, but do not show spontaneous prosocial behavior (Brownell et al., 2009). Our results indicate that in the Costly Sharing Game, older children were overall less likely to choose 1/1 than were younger children, a result that is likely best interpreted as meaning that older children more quickly figured out the fact that there is a unique self-maximizing outcome in the Costly Sharing Game (2/0), but not the other games. Older children may have been more adept at identifying this outcome and thus more consistently chose 2/0 (a similar explanation might also explain the main effects of *Trial* and *Siblings*). However, our results do not indicate strong effects of age on children's prosocial behavior between the ages of 3 and 8, suggesting that by about 3–4 years of age, children differentiate to some degree between the control and test condition in the Prosocial Game and the Costly Sharing Game without prompting by recipients or experimenters. The youngest children in our sample were as likely to behave prosocially as the oldest children that we tested, although the difference scores presented in Fig. 2 imply that there may be some developmental increase in prosocial behavior in the Prosocial Game. Our results also suggest that a desire to provide benefits to others, not only a preference for egalitarian outcomes, guides children's preferences for prosocial outcomes in these tasks. This ontogenetic trajectory is largely consistent with the findings of previous work using other protocols (Birch & Billman, 1986; Thompson et al., 1997). Comparing across studies that use variants of the Prosocial Game, at 18 months of age, children's behavior does not differ qualitatively from the behavior of chimpanzees, but this may begin to change at around 2 years of age as children begin to respond to the desires of the recipient. However, age-related changes in prosocial behavior are weak above the age of 3 years, suggesting that the changes that produce differences in prosocial behavior between children and chimpanzees in this task emerge in children between the ages of 2 and 3 years. We do not claim that, at age 2, children's behavior is equivalent to that of chimpanzees, just that these measures do not distinguish chimpanzees from children of this age.

Other tasks provide more evidence for developmental increases in prosocial behavior among children older than 3, and comparisons across studies suggest that the development of prosocial behavior may be delayed when children are paired with anonymous recipients. Fehr et al. (2008) paired 3–8-year-old children with anonymous recipients from their own class and found that older children were substantially more prosocial and egalitarian than younger children (Fig. 5). Moreover, the effects of age were particularly pronounced in the Costly Sharing Game, in which children's selfish interests conflict with prosocial choices. Similar age effects have been found in anonymous Dictator Games (Harbaugh et al., 2003; Benenson et al., 2007; Gummerum et al., 2009), although not all studies find significant effects of age on allocation decisions (Harbaugh & Krause, 2000; Takezawa et al., 2006; Gummerum, Keller, Takezawa, & Mata, 2008). It is possible that prosocial behavior emerges earlier in face-to-face contexts because recipients are present and can make direct requests for rewards. However, children did not often make requests in our experiments, and requests did not have a substantive impact on actor's behavior. This makes it less likely that children's prosocial behavior in the current experiment was directly analogous to "tolerated theft," in which owners of food share to avoid harassment by others (Stevens & Stephens, 2002; Stevens & Gilby, 2004; Gilby, 2006).

Age effects also emerge when actors must wait to receive rewards. When 3-year-olds were offered a choice between one sticker immediately or one sticker each for themselves and the experimenter at the end of the game, 3-year-old children chose the delayed prosocial option only 10% of the

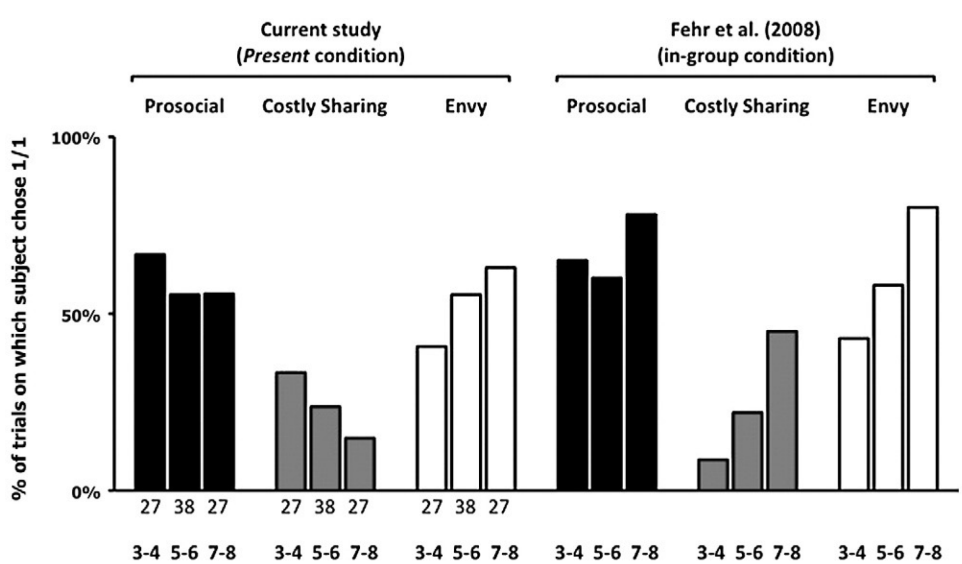

Fig. 5. Children's choices of 1/1 in the present condition of the current study as compared with choices by children in the in-group condition of Fehr et al. (2008). Percentage of trials on which children chose 1/1 are on the vertical axis, while age groups (e.g., 3–4 years) are on the horizontal axis. Black bars are for choices made in the Prosocial Game, gray bars are for the Costly Sharing Game, and white bars are for the Envy Game. Values below each bar correspond to the number of participants in that group.

time. In contrast, 5-year-old children chose the delayed prosocial option about 67% of the time (Thompson et al., 1997). This suggests that for experimental tasks involving delays in the delivery of rewards, ontogenetic changes in children's choices may reflect developmental changes in reasoning about delays in reward, not developmental changes in prosocial behavior.

4.2. Effects of laughter

Although young children were as prosocial as older children in these games, there did seem to be a developmental shift in what children thought was funny. This was reflected in the strong interaction between *Age* and *Laughter*, which indicates that older children found it more amusing *not* to choose 1/1 in these two games. When actors laughed, they were less likely to choose the option that favored the recipient in the present condition. Thus, by choosing 1/0 over 1/1 and 1/1 over 1/2, actors seemed to be making a joke, one that was presumably funny because it contravened a social norm or expectation. The joke itself was not particularly cerebral ("ha ha, you don't get anything!"), but its contrarian nature implies that actors knew that recipients desired or expected the 1/1 distribution, and that actors used this knowledge to inform their choices.

If this joke was funny because it contravened the recipient's desires or expectations, the more clearly contrarian a choice was, the funnier the joke should have been. This might be why the *Condition* × *Laughter* interaction is strongest in the Prosocial Game and weakest in the Costly Sharing Game. Choosing 1/0 over 1/1 in the Prosocial Game or choosing 1/1 over 1/2 in the Envy Game is more clearly contrarian than choosing 2/0 over 1/1 if actors enter the game with the belief that the recipients expect cost-free prosociality. If the actor intentionally chooses 1/0 over 1/1, he/she is clearly doing so only to be contrary. However, in the Costly Sharing Game, the actor might choose 2/0 over 1/1 to maximize his/her own payoff, and the choice is not obviously contrary. It is also likely that choosing 1/0 over 1/1 would be perceived as more contrarian than choosing 1/1 over 1/2 because in the former case, the recipient receives nothing instead of something, while in the latter case, the recipient simply receives relatively less of a reward. These explanations are consistent with the fact that all factors that capture children's laughter (*Laughter*, *Condition* × *Laughter*, and *Age* × *Laughter*) are much more likely to be included in the best model for the Prosocial Game than in the best models for the other games. Children's laughter is thus most important for understanding their behavior in the Prosocial Game.

It has been proposed that laughter and humor are seen when a violation occurs, yet simultaneously the situation is perceived to be "normal" (Veatch, 1998). This is supported by recent experimental work showing that laughter is evoked by violations, such as behavior that is nonnormative, but only when the violation is perceived to be benign in its consequences (McGraw & Warren, 2010). Our results fit this scenario because the effect of *Laughter* is strongest when a normative violation has most obviously occurred. It is also quite likely that young children in our experiments viewed the loss of a single Goldfish cracker as a relatively benign outcome that entailed little real harm.

4.3. Effects of sex

Actor's sex has a significant effect on children's behavior in the Costly Sharing Game, but not in the other two games. The Costly Sharing Game differs from the other two games because actors must give up rewards to confer rewards on their partners. In this game, females were substantially more likely to choose the prosocial option in the present condition than males. Our findings fit reasonably well with evidence from the developmental literature on prosocial behavior, which generally indicates that females are more prosocial than males (Eisenberg & Fabes, 1998). While the main effect of actor's sex is not likely to be included in the best model for the Costly Sharing Game on its own, our analyses suggest that the interaction between actor's sex and *Condition* is important for understanding children's behavior.

The interaction between *Sex* and *Condition* in the Costly Sharing Game also parallels results that have emerged in studies of adults and children in the Dictator Game. In the Dictator Game, one player is given an endowment and allowed to send some portion of that endowment anonymously to a second player. Thus, the Costly Sharing Game is formally a discrete Dictator Game. Among adults, females are more willing than males to incur costs to allocate payoffs to a recipient, females are less averse to inequality than males, and females are less sensitive to efficiency than males (reviewed by Croson & Gneezy, 2009). The efficiency of a donation describes how the cost to the donor relates to the benefit conferred on the recipient. For example, a donation is efficient if it confers three units of payoff for every two units of cost, but inefficient if it confers one unit of payoff to a recipient for every two units of cost to the donor. In Dictator Games conducted with children, females generally are more likely to donate or donate larger amounts than males (Harbaugh et al., 2003; Gummerum et al., 2008, 2009; Leman, Keller, Takezawa, & Gummerum, 2009; Blake & Rand, 2010). Moreover, in an experiment in which children played a Dictator Game in which the efficiency of donations was manipulated, 14–18 year-old males were more sensitive to efficiency than females of the same ages (Almas, Cappelen, Sorensen, & Tungodden, 2010). However, not all experimental economic studies conducted with children found such sex differences (Harbaugh & Krause, 2000; Sally & Hill, 2006; Takezawa et al., 2006; Benenson et al., 2007; Lucas, Wagner, & Chow, 2008).

4.4. Effects of trial and siblings

Children were less likely to choose 1/1 in all three games as trial number increased, but these effects were most pronounced in the Costly Sharing Game. As with *Age*, the main effect of *Trial* may be due to the fact that there was a unique self-maximizing outcome in the Costly Sharing Game (2/0). Children might have become better able to recognize the consequences of their choices as the experiment progressed, and this might have enhanced the likelihood of choosing the self-maximizing outcome in later trials. Consistent with this, *Trial* is very likely to be found in the best model for the Costly Sharing Game and thus is important for understanding children's behavior in this task.

Similarly, children with siblings might have more experience with resource distribution problems than children without siblings. This might be why children with siblings were substantially more likely to choose the 2/0 option in the Costly Sharing Game than only children. Fehr et al. (2008) reported a similar effect of having siblings in the Costly Sharing Game. In both the Prosocial and Envy Games, there is a weak effect of *Siblings*, but in the Envy Game, there is also a strong interaction between *Condition* and *Siblings*. Children with siblings chose 1/1 substantially more on trials in the present condition relative to only children and more than all children chose 1/1 in the absent condition. This suggests that children with siblings were more egalitarian than children without siblings. However, *Siblings* is likely to be important for interpreting children's behavior in the Prosocial and Costly Sharing Games, and *Condition* × *Siblings* is only somewhat likely to be important in the Costly Sharing Game.

5. Summary

In conclusion, our results suggest that even very young children differ from chimpanzees in situations in which they must make choices about the distribution of valued rewards in face-to-face settings. By the age of 3–4 years, children seem to be sensitive to the impact of their choices on their own welfare—they distinguish between high-value and low-value rewards, and they choose the 1/1 option more in the Prosocial Game than in the Costly Sharing Game. By the same age, children seem to have a spontaneous preference for prosocial outcomes when they are face-to-face with recipients and will receive rewards immediately. Our results suggest that a desire to provide benefits to others, not only a preference for egalitarian outcomes, guides children's preferences for prosocial outcomes in these tasks. Children's laughter in the Prosocial Game suggests that they are aware of the normative expectations about behaving prosocially and that they find it amusing to violate these norms. Comparisons across the full range of studies of children using similar types of distribution tasks suggest that young children are more strongly influenced by the physical presence of recipients and the immediate distribution of rewards than older children, perhaps because the needs and desires of others are more salient to young children in face-to-face encounters than in anonymous settings. Egalitarian preferences seem to emerge somewhat later than prosocial preferences and may be more pronounced in anonymous settings than face-to-face interactions.

Acknowledgments

We greatly thank Richard McElreath for advice on data analysis, and also numerous anonymous reviewers and the editor for helpful comments. Support for this research was provided by the UCLA NSF IGERT Interdisciplinary Relationship Science Program (B.R.H.).

References

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In B. N. Petrov, & F. Csaki (Eds.), *Second International Symposium of Information Theory* (pp. 267-281). Hungary: Akademiai Kiado, Budapest.

Alexander, R. D. (2006). The challenge of human social behavior. *Evolutionary Psychology*, *4*, 1–32.

Almas, I., Cappelen, A. W., Sorensen, E. O., & Tungodden, B. (2010). Fairness and the development of inequality acceptance. *Science*, *328*, 1176–1178.

Axelrod, R., & Hamilton, W. (1981). The evolution of cooperation. *Science*, *211*, 1390–1396.

Batson, C. D. (1987). Prosocial motivation: is it ever truly altruistic? *Advances in Experimental Social Psychology*, *20*, 65–122.

Batson, C. D. (1991). The Altruism question: toward a social psychological answer. Hillsdale, NJ: Erlbaum.

Batson, C. D., Duncan, B. D., Ackerman, P., Buckley, T., & Birch, K. (1981). Is empathic emotion a source of altruistic motivation? *Journal of Personality and Social Psychology*, *40*, 290–302.

Benenson, J. F., Pascoe, J., & Radmore, N. (2007). Children's altruistic behavior in the dictator game. *Evolution and Human Behavior*, *28*, 168–175.

Birch, L. L., & Billman, J. (1986). Preschool children's food sharing with friends and acquaintances. *Child Development*, *57*, 387.

Blake, P. R., & Rand, D. G. (2010). Currency value moderates equity preference among young children. *Evolution and Human Behavior*, *31*, 210–218.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, *78*, 547–573.

Bowles, S. (2006). Group competition, reproductive leveling, and the evolution of human altruism. *Science*, *314*, 1569–1572.

Bowles, S., & Gintis, H. (2004). The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theoretical Population Biology*, *65*, 17–28.

Boyd, R., Gintis, H., Bowles, S., & Richerson, P. J. (2003). The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 3531–3535.

Boysen, S. T., & Berntson, G. G. (1995). Responses to quantity: perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology-Animal Behavior Processes*, *21*, 82–86.

Boysen, S. T., Berntson, G. G., Hannan, M. B., & Cacioppo, J. T. (1996). Quantity-based interference and symbolic representations in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology-Animal Behavior Processes*, *22*, 76–86.

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*, *12*, 587–597.

Brownell, C. A., Svetlova, M., & Nichols, S. (2009). To share or not to share: when do toddlers respond to another's needs? *Infancy*, *14*, 117–130.

Burkart, J. M., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences*, *104*, 19762–19766.

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: a practical information-theoretic approach. New York, NY: Springer Verlag.

Croson, R., & Gneezy, U. (2009). Gender differences in preferences. *Journal of Economic Literature*, *47*, 448–474.

de Waal, F. B. M. (1997a). Good natured: the origins of right and wrong in humans and other animals. Cambridge, MA: Harvard University Press.

de Waal, F. B. M. (1997b). The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, *18*, 375–386.

de Waal, F. B. M. (2009). The age of empathy: nature's lessons for a kinder society. Toronto, CA: McClelland & Stewart.

Dunbar, R. I. M. (2008). Kinship in biological perspective. In N. J. Allen, & H. Callan, & R.I.M. Dunbar, & W. James (Eds.), *Early human kinship: from sex to social reproduction* (pp. 131–150). Oxford, UK: Blackwell.

Eisenberg, N., & Fabes, R. A. (1998). Prosocial development. *Handbook of child psychology*, *3*, 701–778.

Fehr, E., Bernhard, H., & Rockenbach, B. (2008). Egalitarianism in young children. *Nature*, *454*, 1079–1083.

Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, *425*, 785–791.

Fehr, E., & Fischbacher, U. (2004). Social norms and human cooperation. *Trends in Cognitive Sciences*, *8*, 185–190.

Fehr, E., & Gachter, S. (2002). Altruistic punishment in humans. *Nature*, *415*, 137–140.

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour*, *71*, 953–963.

Gintis, H., Bowles, S., Boyd, R., & Fehr, E. (2003). Explaining altruistic behavior in humans. *Evolution and Human Behavior*, *24*, 153–172.

Gintis, H., Smith, E. A., & Bowles, S. (2001). Costly signaling and cooperation. *Journal of Theoretical Biology*, *213*, 103–119.

Greenberg, J. R., Hamann, K., Warneken, F., & Tomasello, M. (2010). Chimpanzee helping in collaborative and noncollaborative contexts. *Animal Behaviour*, *80*, 873–880.

Gummerum, M., Hanoch, Y., Keller, M., Parsons, K., & Hummel, A. (2009). Preschoolers' allocations in the dictator game: the role of moral emotions. *Journal of Economic Psychology.*

Gummerum, M., Keller, M., Takezawa, M., & Mata, J. (2008). To give or not to give: children's and adolescents' sharing and moral negotiations in economic decision situations. *Child Development*, *79*, 562–576.

Gurven, M. (2004). To give and to give not: the behavioral ecology of human food transfers. *Behavioral and Brain Sciences*, *27*, 543–559.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*, 1–16.

Harbaugh, W. T., & Krause, K. (2000). Children's altruism in public good and dictator experiments. *Economic Inquiry*, *38*, 95–109.

Harbaugh, W. T., Krause, K., & Liday, S. G. (2003). Bargaining by children (working paper). Eugene, Oregon: University of Oregon, Department of Economics.

Harbaugh, W. T., Krause, K., & Vesterlund, L. (2007). Learning to bargain. *Journal of Economic Psychology*, *28*, 127–142.

Hay, D. F., Castle, J., Davies, L., Demetriou, H., & Stimson, C. A. (1999). Prosocial action in very early childhood. *Journal of Child Psychology and Psychiatry*, *40*, 905–916.

Henrich, J. (2004). Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior & Organization*, *53*, 3–35.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., & Gintis, H., et al. (2005). "Economic man" in cross-cultural perspective: behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences*, *28*, 795–815.

Henrich, J., Ensminger, J., McElreath, R., Barr, A., Barrett, C., & Bolyanatz, A, et al. (2010). Markets, religion, community size, and the evolution of fairness and punishment. *Science*, *327*, 1480–1484.

Henrich, J., McElreath, R., Barr, A., Ensminger, J., Barrett, C., & Bolyanatz, A, et al. (2006). Costly punishment across human societies. *Science*, *312*, 1767–1770.

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. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 1013–1021.

Leman, P. J., Keller, M., Takezawa, M., & Gummerum, M. (2009). Children's and adolescents' decisions about sharing money with others. *Social Development*, *18*, 711–727.

Lucas, M. M., Wagner, L., & Chow, C. (2008). Fair game: the intuitive economics of resource exchange in four-year olds. *Journal of Social, Evolutionary, and Cultural Psychology*, *2*.

Marlowe, F. W., Berbesque, J. C., Barr, A., Barrett, C., Bolyanatz, A., & Cardenas, J. C., et al. (2008). More "altruistic" punishment in larger societies. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 587–592.

McElreath, R., Bell, A. V., Efferson, C., Lubell, M., Richerson, P. J., & Waring, T. (2008). Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*, 3515–3528.

McGraw, A. P., & Warren, C. (2010). Benign violations. *Psychological Science*, *21*, 1141–1149.

McNamara, J. M., Barta, Z., Fromhage, L., & Houston, A. I. (2008). The coevolution of choosiness and cooperation. *Nature*, *451*, 189–192.

Melis, A. P., Warneken, F., Jensen, K., Schneider, A. C., Call, J., & Tomasello, M (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 1405.

Mitani, J. C. (2006). Reciprocal exchange in chimpanzees and other primates. In C. P. van Schaik, & P. M. Kappeler (Eds.), *Cooperation in primates and humans* (pp. 107–119). Heidelberg: Springer Verlag.

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*, 633–640.

Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, *61*, 915–924.

Moore, C. (2009). Fairness in children's resource allocation depends on the recipient. *Psychological Science*, *20*, 944–948.

Muller, M. N., & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior*, *35*, 275–331.

Murnighan, J. K., & Saxon, M. S. (1998). Ultimatum bargaining by children and adults. *Journal of Economic Psychology*, *19*, 415–445.

Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y., & Uehara, S. (1992). Meat-sharing as a coalition strategy by an alpha male chimpanzee. *Topics in primatology*, *1*, 159–174.

Nishida, T., & Turner, L. A. (1996). Food transfer between mother and infant chimpanzees of the Mahale Mountains National Park. *TanzaniaInt J Primatol*, *17*, 947–968.

Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, *437*, 1291–1298.

Sally, D., & Hill, E. (2006). The development of interpersonal strategy: autism, theory-of-mind, cooperation and fairness. *Journal of Economic Psychology*, *27*, 73–97.

Silk, J. B. (2009). Social preferences in primates. In P. W. Glimcher, & C. F. Camerer, & E. Fehr, & R. A. Poldrack (Eds.), *Neuroeconomics: decision making and the brain* (pp. 269–284). London, UK: Academic Press.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., & Richardson, A. S., et al. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, *437*, 1357–1359.

Silk, J. B., & House, B. R. (2011). Colloquium paper: Evolutionary foundations of human promoral sentiments. *Proceedings of the National Academy of Sciences*, *108*, 10910–10917.

Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for nonkin food sharing: timing and currency of benefits. *Animal Behaviour*, *67*, 603–614.

Stevens, J. R., & Stephens, D. W. (2002). Food sharing: a model of manipulation by harassment. *Behav Ecol*, *13*, 393–400.

Takezawa, M., Gummerum, M., & Keller, M. (2006). A stage for the rational tail of the emotional dog: roles of moral reasoning in group decision making. *Journal of Economic Psychology*, *27*, 117–139.

Thompson, C., Barresi, J., & Moore, C. (1997). The development of future-oriented prudence and altruism in preschoolers. *Cognitive Development*, *12*, 199–212.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, *46*, 35.

Veatch, T. C. (1998). A theory of humor. *Humor-International Journal of Humor Research*, *11*, 161–216.

Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., & Lambeth, S. P., et al. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*, *75*, 1757–1770.

Warneken, F., Hare, B., Melis, A. P., Hanus, D., & Tomasello, M. (2007). Spontaneous altruism by chimpanzees and young children. *PLoS Biology*, *5*, e184.

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science*, *311*, 1301–1303.

Warneken, F., & Tomasello, M. (2009). Varieties of altruism in children and chimpanzees. *Trends in Cognitive Sciences*, *13*, 397–402.

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, *44*, 43–55.

Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*, 299–327.

Yamamoto, S., & Tanaka, M. (2010). The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. *Animal Behaviour*, *79*, 595–602.

Zahn-Waxler, C., & Radke-Yarrow, M. (1990). The origins of empathic concern. *Motivation and Emotion*, *14*, 107–130.

Zahn-Waxler, C., Radke-Yarrow, M., Wagner, E., & Chapman, M. (1992). Development of concern for others. *Developmental Psychology*, *28*, 126–136.