Original Article

Capuchin monkeys punish those who have more

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ABSTRACT

Punishment of non-cooperators is important for the maintenance of large-scale cooperation in humans, but relatively little is known about the relationship between punishment and cooperation across phylogeny. The current study examined second-party punishment behavior in a nonhuman primate species known for its cooperative tendencies—the brown capuchin monkey (*Cebus apella*). We found that capuchins consistently punished a conspecific partner who gained possession of a food resource, regardless of whether the unequal distribution of this resource was intentional on the part of the partner. A non-social comparison confirmed that punishment behavior was not due to frustration, nor did punishment stem from increased emotional arousal. Instead, punishment behavior in capuchins appears to be decidedly social in nature, as monkeys only pursued punitive actions when such actions directly decreased the welfare of a recently endowed conspecific. This pattern of results is consistent with two features central to human cooperation: spite and inequity aversion, suggesting that the evolutionary origins of some human-like punitive tendencies may extend even deeper than previously thought.

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1. Introduction

Cooperation is central to human societies, and the punishment of non-cooperators is thought to play a key role in both the emergence (Boyd, Gintis, Bowles, & Richerson, 2003) and maintenance of cooperation within social communities (Boyd, Gintis, & Bowles, 2010). While self-serving strategies quickly proliferate in the absence of punitive options (e.g., Boyd et al., 2003; Fehr & Gächter, 2002), the mere threat of punishment (Fehr & Gächter, 2002; Gintis, Smith, & Bowles, 2001) as well as negative gossip that may lead to punishment (Beersma & Van Kleef, 2011; Ellingsen & Johannesson, 2008; Piazza & Bering, 2008) is sufficient to deter selfish individuals from profiting at the expense of the group. Accordingly, many researchers have argued that punishment of non-cooperative individuals can uphold group cooperative norms by dissuading recidivist non-cooperators, while also signaling to others in the group that such violations will not be tolerated (Clutton-Brock & Parker, 1995).

Accordingly, research shows that human adults routinely engage in punitive actions, even when such actions are personally costly or are undertaken to benefit a group rather than the individual in the case of "altruistic" punishment (Fehr & Fischbacher, 2004; Fehr & Gächter, 2000; Fehr & Gächter, 2002; Gürerk, Irlenbusch, & Rockenbach, 2006). This raises important questions concerning why individuals would willingly bear the immediate burden of punishment for the long-term

benefit of the group. More specifically, what psychological motivations lead individuals to engage in costly punitive actions? Importantly, both second-party punishment (when one has a self-interested stake) and third-party punishment (as an unaffected observer) depend on the actor having the urge to punish and may share common psychological roots (Buckholtz & Marois, 2012). A growing body of research suggests that people's decisions to punish others are sensitive to a number of social and psychological factors. That is, human punishment is often selective: people are more likely to engage in costly punitive behaviors when certain psychological conditions are met.

First, people take into account the intentions of a transgressor when making judgments about blameworthiness (Nelson, 2002). Specifically, decision-makers tend to punish those perceived to have malintent more than those with good intentions, even when the negative outcomes are equated (Charness & Levine, 2003). The evaluation of intentions is particularly relevant in punishment of fairness violations, as several studies show that unfair outcomes are punished most harshly when they come about as the result of unfair intentions (Falk, Fehr, & Fischbacher, 2008; Fehr & Schmidt, 1999; Rabin, 1993). Second, individual decisions to engage in punishment are driven by egocentric motivations. In fact, much of the punitive behavior in which humans engage is motivated by feelings of personal – not social – injustice. People punish others out of revenge (e.g. Bone & Raihani, 2015; Cota-McKinley, Woody, & Bell, 2001), spite (e.g. Abbink & Herrmann, 2011; Abbink & Sadrieh, 2009), or simply because of an aversion to having less than others (e.g. Johnson, Dawes, Fowler, McElreath, & Smirnov, 2009). Indeed, research suggests that an aversion to personally disadvantageous outcomes plays a large role in driving punishment in adults (Raihani &

McAuliffe, 2012); this notion is supported by evidence that those engaging in punishment behavior often do so not to achieve equality, but to create inequality in their own favor (Houser & Xiao, 2010). Third, people are more likely to engage in punishment when they experience certain emotional states, such as anger or moral disgust. For example, individuals are more likely to punish others who make unfair offers when they feel anger in response to that person's behavior (Pillutla & Murnighan, 1996; Xiao & Houser, 2005). Finally, people consider how their actions are likely to be perceived by other parties when making punishment decisions. In particular, people are more likely to engage in costly punishment of moral violations in the presence of a social audience than in anonymous situations (Kurzban, DeScioli, & O'Brien, 2007). In this way, punishment can potentially allow actors to reap positive social benefits associated with being seen as a cooperative individual in the eyes of fellow group members.

There is also increasing evidence that punishment behaviors – and this suite of psychological motivations underlying them – emerge fairly early in development. Indeed, even young children will punish others by avoiding social interactions with them, or redistributing resources away from them. For example, when given the option, toddlers systematically direct their own negative actions towards an antisocial individual over a prosocial one (Hamlin & Wynn, 2011). Around 3–4 years of age, children begin acting less prosocially toward people whom they've seen harm or intend to harm another individual (Kenward & Dahl, 2011; Vaish, Carpenter, & Tomasello, 2010), and tattle on puppets whom they've witnessed committing moral violations (Vaish, Missana, & Tomasello, 2011). Finally, by the age of 5, children appear willing to take a personal cost to punish those who exhibit non-cooperative tendencies (McAuliffe, Jordan, & Warneken, 2015; Robbins & Rochat, 2011).

More importantly, recent evidence suggests that young children's resource distribution and punishment decisions appear sensitive to the same psychological motivations that underlie punishment decisions in adults. First, children pay attention to the intentions of actors when making punitive judgments, much like adults. Even 8-month-old infants distinguish between actors who cause bad outcomes because of bad intentions and those who bring about bad outcomes accidently (Hamlin, 2013), and children begin to incorporate information about other's intentions into their naughtiness and punishability judgments between 4 and 8 years of age (Cushman, Sheketoff, Wharton, & Carey, 2013). Second, there is growing evidence that young children show spiteful preferences and are willing to take a cost to achieve resource distributions that personally benefit them (McAuliffe, Blake, & Warneken, 2014; Sheskin, Bloom, & Wynn, 2014). Finally, by the age of 5, children are sensitive to the presence of a social audience when making decisions tied to norms of cooperation and fairness (Engelmann, Herrmann, & Tomasello, 2012; Leimgruber, Shaw, Santos, & Olson, 2012; McAuliffe, Blake, Kim, Wrangham, & Warneken, 2013). These results have led some researchers to suggest that the presence of an audience and, relatedly, reputational concerns may influence many aspects of children's cooperative decisions even early in life (Shaw, Li, & Olson, 2013).

Taken together, this work suggests that some of the psychological motivations underlying adult human punishment – factors like understanding the intentions of others, considerations regarding relative resource distributions, and reputational concerns – are in place very early in human development. Given this pattern of early emergence in humans, these types of responses likely depend at least in part on foundational social cognitive skills that are shared with other species, such as the ability to judge other's intentions (Call, Hare, Carpenter, & Tomasello, 2004; Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009). However, while the psychological factors that promote punishment in our own species have been the focus of intense research, the evolutionary origins of the capacities supporting punishment are less well understood. In fact, many comparative studies of punishment in nonhumans typically define punishment as behaviors that impose an immediate cost on others to decrease the occurrence of an undesirable

behavior (Clutton-Brock & Parker, 1995). Using this definition, examples of punishment behavior in non-human animals are relatively rare, even in primates (for one exception in fish, see Raihani, Thornton, & Bshary, 2012). Several species of non-human primates appear to engage in retributive behavior in reaction to harm to themselves or closely-affiliated others (Aureli et al., 1992; Crofoot & Wrangham, 2010; de Waal, 1982). However, these studies focus on whether such behaviors occur, and not the *psychological motivations* that underlie primates' punitive behaviors.

One important exception is a set of studies examining punitive tendencies in chimpanzees (Jensen, Call, & Tomasello, 2007; Riedl, Jensen, Call, & Tomasello, 2012). Jensen et al. (2007) investigated the circumstances under which chimpanzees would collapse a table to prevent a conspecific from accessing food. In fact, chimpanzees were more likely to collapse the table when their partner had initially stolen the resource, compared to when an experimenter had redistributed the resource—suggesting that the chimpanzees, like humans, were sensitive to the intentions of the actor. Interestingly, chimpanzees were not willing to punish when the same transgressions happened to a third party (Riedl et al., 2012). Overall, these results suggest that chimpanzees use punishment as a means of retaliation for direct personal harm, an explanation supported by evidence that behavioral signs of arousal correlated with increased punishment behavior (Jensen et al., 2007).

The results from Jensen and colleagues indicate that chimpanzees share some of psychological mechanisms underlying punishment in humans. However, chimpanzees are not the only primate species that can provide insights into the relationship between punishment and the evolution of cooperation. In fact, chimpanzees show important divergences from humans in some aspects of their social behavior. Although chimpanzees have relatively sophisticated perspective-taking abilities (Call & Tomasello, 2008) and are capable of recognizing cues of need in others (Melis & Tomasello, 2013; Melis et al., 2011; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2006), chimpanzees and humans differ in patterns of prosociality. For example, chimpanzees are often indifferent to opportunities to donate food to conspecifics at no personal cost (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005; Vonk et al., 2008, but see Horner, Carter, Suchak, & de Waal, 2011 for an exception) Consequently, studies of species that more consistently engage in cooperative and prosocial behaviors are critical for understanding the evolution of a human-like punishment psychology, and its relationship to cooperation more generally.

Here, we aimed to disentangle the importance of motivations underlying punishment behavior in a primate species known to engage in rich cooperative behaviors—the brown capuchin monkey (*Cebus apella*) (Brosnan, 2010; Hattori, Kuroshima, & Fujita, 2005). Capuchin monkeys more consistently exhibit other-regarding tendencies in donation tasks than chimpanzees (de Waal & Suchak, 2010; de Waal, Leimgruber, & Greenberg, 2008; Lakshminarayanan & Santos, 2008; Takimoto, Kuroshima, & Fujita, 2010, although see Drayton & Santos, 2014 for an exception), and are sensitive to social disparity in outcomes (Brosnan, 2011; Brosnan, Freeman, & De Waal, 2006). There is also evidence that capuchin monkeys avoid non-reciprocators when making affiliative decisions (Anderson, Takimoto, Kuroshima, & Fujita, 2013) and cease participation in a joint-pulling task when it is likely that the cooperative partner will monopolize the reward (de Waal & Davis, 2003, see also Brosnan et al., 2006). Taken together with evidence that capuchins modify their social behavior when visually and audibly isolated from conspecifics (de Waal et al., 2008; Pollick, Gouzoules, & de Waal, 2005), this set of findings suggests that capuchin monkeys are a strong phylogenetic model of the human-like relationship between punishment and cooperation.

Using a method modeled after that used with chimpanzees (Jensen et al., 2007), we assessed the importance of the factors that influence human punishment on the monkeys' punishment decisions. In particular, we examined how monkeys responded to inequality of reward

outcomes (i.e., having less of a reward than another monkey), the intentionality of the benefactor (i.e., having a resource deliberately stolen), the importance of emotional arousal as indexed by scratching (a common measure of stress or arousal in primates; Maestripieri, Schino, Aureli, & Toisi, 1992; Polizzi di Sorrentino, Schino, Tiddi, & Aureli, 2012), and the presence of an audience proximate to the social interaction. Here we focused on second-party punishment, given that there is currently no evidence for robust third-party punishment in nonhumans. Importantly, such second-party punishment behaviors have been suggested to represent the evolutionary roots of human punishment behaviors (Buckholtz & Marois, 2012). Overall, this approached allowed us to disentangle which psychological motivators of human punishment behaviors are shared with capuchins by modeling which of these factors best predicted the capuchins' likelihood of punishing a conspecific.

2. Methods and materials

2.1. Participants

We tested 6 brown capuchin monkeys (*Cebus apella*) ranging in age from 6 to 17 years (3 males [AH, FL, NN], 3 females [HG, JM, MD]; M_{age} = 166.8 months, SD = 52.41). All monkeys were familiar with one another prior to testing, as they were socially housed as part of a nine-member group that comprised the Yale Comparative Cognition Laboratory. This indoor enclosure was equipped with natural branches and toys, and had access to water and food ad libitum. An additional monkey who was the lowest ranking adult member of the social group – a 7-year-old female [HR] – acted as the partner stooge for all individuals; we chose this individual to act as the stooge because previous research suggests that chimpanzees are more likely to punish group members of a lower social rank (Jensen et al., 2007). Two of the subjects were related to the partner stooge: her mother [HG] and her brother [AH]. One juvenile monkey in the colony ([HB], *age* = 4 years) was not tested in the study due to her immature age, and a second female monkey ([MP], *age* = 5 years) was excluded from the study after failing to reliably collapse the table in the Habituation stage of testing. All studies were approved by the Yale University Institutional Animal Care and Use Committee.

2.2. Testing apparatus and experimental setup

For all test sessions, subjects were physically isolated from the social group and given sole access to a section of their habitat that included an adjacent, smaller testing enclosure (71 cm^3). In conditions where the stooge monkey was present, the stooge was moved into an identical testing enclosure placed opposite to the one accessible to the subject. A wooden table (76 cm long × 51 cm wide × 46 cm high) was situated between the two testing enclosures such that each monkey could comfortably reach the top of it through the mesh sides of their own enclosures. One side of the table contained a hinged leaf (51 cm × 25 cm) held up by a false leg; removal of the false leg caused the leaf to collapse and anything atop it to fall into a shallow container situated on the table below the leaf (which was out of reach of both the subject and the stooge). A rope attached to the false leg was strung through the front of the larger testing area so subjects could access it during test trials (Fig. 1). Across most conditions, the table was situated such that the collapsible leaf was nearest to the stooge's testing enclosure; however, in the Comprehension Pretest, the table was situated with the collapsible leaf closer to the subject on half of the trials.

During test trials, a removable tray containing approximately 1/2 cup of Fruity Pebbles® cereal – a highly valued food reward in this population of capuchin monkeys – was placed atop the table. The cereal was loosely affixed to the tray with a thin layer marshmallow fluff, and was replenished so that the tray held a consistent volume of cereal across trials. The cereal could be made accessible to the subject or the stooge
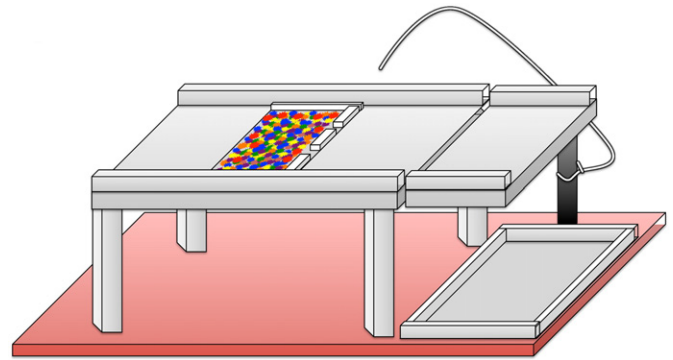

Fig. 1. Side-view of the collapsible table.

simply by pushing the tray flush with the front of the target monkey's enclosure. The size of the mesh on the enclosures was such that subjects could only get one finger through each opening, considerably slowing their ability to eat the cereal in large quantities. As a result, subjects were only able to retrieve a small handful of cereal (roughly five individual Fruity Pebbles) on each trial before the tray was moved. Additionally, the tray was situated on the table such that the actor and stooge monkeys foraged off opposite sides when the tray was made available to them; as a result, the amount of cereal the actor was able to eat prior to the food loss event in no way impacted the amount of food available to the stooge.

2.3. General methods

Prior to the commencement of testing, all six subjects completed a Habituation session and a Comprehension Pretest session. The stooge completed 3 days of training in which she quickly learned to pull the rope to attain the tray of cereal when it was made available to her. The stooge reliably pulled the rope and ate food from the tray in all subsequent sessions when she was paired opposite conspecifics.

2.3.1. Habituation phase

The goal of the Habituation phase was 1) to ensure that subjects were physically capable of pulling the rope and collapsing the table, and 2) to expose subjects to the outcome resulting from the table's collapse (e.g., the items on the table falling out of reach of both the actor and the recipient). Here, monkeys were able to collapse a tray containing a non-edible item (a length of plastic chain) in order to see how the tray's contents dropped out of reach when the table was collapsed. Subjects were first centered in their testing enclosure using a small piece of Kix® cereal, and then an experimenter placed the length of rope attached to the collapsible leg through the front of the larger testing area while calling the subject's name to attract the monkey's attention. The experimenter then placed the tray (containing the plastic chain) atop the testing apparatus, slid it onto the collapsible portion of the table, and gave the subject the Kix to signal the start of the trial. Subjects were given 3 min to collapse the table of their own accord. If they did not do so in this timeframe, the experimenter drew attention to the rope by wiggling it and calling the subject's name aloud. If this did not prompt the subject to pull the rope, the experimenter attached a small piece of Kix to the rope after an additional 2 min (to prompt them to pull it to obtain the cereal). Subjects passed the Habituation phase when they successfully pulled the rope to collapse the table 4 times. This phase therefore ensured that all subjects had experienced pulling the tray and seeing its contents drop out of reach an equal number of times before they moved on to the Comprehension Pretest.

All subjects included in the current study successfully met criteria within one test session ($M_{session\ length}$ = 746.69 s, SE = 219.26; $M_{latency\ to\ first\ pull}$ = 304.86 s, SE = 120.54; $M_{latency\ per\ pull}$ = 146.55 s; SE = 23.37). One additional subject [MP] was excluded from the study for

failing to consistently collapse the table after 4 test sessions (total testing time = 3704.63 s). Individual Habituation pulling data can be found in Table S1 in the electronic supplemental materials (available on the journal's website at www.ehbonline.org).

2.3.2. Comprehension pretest

The purpose of the Comprehension Pretest was to: 1) confirm that subjects understood the basic setup and would not collapse the table on themselves when they had access to the food, and 2) to attain a baseline measure of the rate at which each subject collapsed the table when another monkey had access to the food. The Pretest session was comprised of 12 60-s trials: 6 Self-Feeding trials in which the subject had access to the food tray (Figure S1a, available on the journal's website at www.ehbonline.org) and 6 Other-Feeding trials in which the stooge had access to the food tray (Figure S1b, available on the journal's website at www.ehbonline.org). For Self-Feeding trials, the table was situated such that the collapsible portion of the table was in front of the subject's testing enclosure; for the Other-Feeding trials, the table was situated such that the collapsible portion of the table was in front of the stooge's testing enclosure. As a result, subjects who collapsed the table during the Self-Feeding trials caused the cereal to fall out of their own reach, whereas collapsing the table during the Other-Feeding trials resulted in the stooge losing access to the cereal; both Self- and Other-Feeding trials required the subject to leave his/her own immediate testing enclosure to pull the rope to collapse the table.

The monkeys completed a block of six trials per trial type (in a single session of 12 trials), with condition order counterbalanced across subjects. In each trial, the subject was centered in his/her testing enclosure using a small piece of Kix cereal after which an experimenter placed the length of rope attached to the collapsible leg through the front of the large testing area while calling the subject's name to attract his/her attention. The experimenter then placed the tray containing Fruity Pebbles cereal on the testing apparatus and moved it until it was flush with the appropriate monkey's testing enclosure.

Overall, subjects never collapsed the table when they had access to food (Self-Feeding trials) versus Mean ± SE = 44.4% ± 8.40 of trials in which only the stooge had access to the food (Other-Feeding trials), a significant difference (Wilcoxon signed-ranks test: Z = −2.02, p < 0.05). This indicates that monkeys understood the general testing set-up and refrained from collapsing the table when they had direct access to the food. Importantly, while no monkey ever pulled the rope in the Self-Feeding trials, the frequency with which individuals collapsed the table in Other-Feeding trials varied between subjects (Table S1, available on the journal's website at www.ehbonline.org). As described in subsequent sections, we therefore used each individual's number of pulls in the Other-Feeding trials of the Comprehension Pretest as a covariate in the main analyses; this allowed us account for individual variation in general propensity to collapse the table.

2.3.3. Test sessions

Each test session was comprised of eight identical trials in which the subject had 60 s to collapse the table. Each trial began after the experimenter presented the tray of cereal to the subject, placed the rope attached to the false leg through the front of the large testing area to which the subject had access, and slid the tray of cereal flush with the front of the appropriate monkey's testing enclosure. Each session consisted of one of four possible test conditions:

Loss Condition   Subjects initially had access to the tray of cereal for 5 s. The trial started when the experimenter moved the tray across the table and flush with the opposite testing enclosure (which was empty), and out of the subject's reach. Because the stooge was not present, this condition measured subjects' frustration at an inaccessible food resource

Partner Feeding Condition   Subjects were centered in the testing enclosure using a single piece of Kix cereal. The trial started when the experimenter slid the tray of cereal across the table and within reach of the stooge monkey. The subject never had access to the food in this condition, thus it measured subjects' responses to the presence of a feeding conspecific.

Outcome Disparity Condition   Subjects had access to the tray of cereal for 5 s, at which point the experimenter moved the tray across the table and within reach of the stooge. This condition assessed how often monkeys collapsed the table in response to the loss of food to the stooge.

Theft Condition   Subjects had access to the tray of cereal for 5 s, at which point the stooge was given access to a rope that allowed her to play a causal role and to "steal" the food, pulling the tray across the table and flush with her testing enclosure. This condition assessed how often monkeys collapsed the table after a conspecific directly caused them to lose access to their food.

Subjects were randomly assigned to one of two testing sequences that dictated the order in which they participated in each of the 4 test conditions (Order A: Loss, Outcome Disparity, Partner Feeding, Theft; Order B: Partner Feeding, Theft, Loss, Outcome Disparity). Assignment to the testing orders was counterbalanced such that half of the subjects were in Order A (AH, HG, JM) and half of the subjects were in Order B (FL, MD, NN).

2.3.4. Audience manipulation

We assessed the importance of social context on monkeys' pulling behavior by manipulating the physical proximity, and thus the ease with which the subjects' social group could view his/her actions in the study. In No Audience sessions, monkeys in the social group were restricted to the areas of the habitat furthest from the testing area to maximize physical distance and minimize visual access to the subject. Specifically, the social group was approximately 2 m away from the subject in the No Audience sessions and there were no shared walls through which the subject could make contact with members of the social group (see Fig. 2a). In the Audience sessions, the areas closest to the subject were accessible to the social group and monkeys were free to come and go as they pleased. Specifically, members of the social group were approximately 1 m away from subject, who was able to make physical contact with other monkeys through the shared mesh wall (see Fig. 2b). Members of the larger social group had access to other food resources in their common area, such that feeding conspecifics were always present in the habitat across conditions. It should be noted that all testing was performed in an isolated area of the monkeys' home habitat, which was constructed of semi-transparent mesh material. As a result, subjects were never *completely* visually or audibly isolated from the social group, however, visual contact was notably minimized in the No Audience sessions; however, previous research has shown evidence of audience effects on social behavior in group-housed capuchin monkeys, even when subjects were not completely visually or audibly isolated (de Waal et al., 2008; Pollick et al., 2005).

The presence of an audience was manipulated via an ABA design, meaning subjects first completed all four conditions with No Audience (NA1), then all four conditions with an Audience (A), and finally all four with No Audience again (NA2). This ABA design allowed us to obtain a baseline measure of each subject's tendency to collapse the
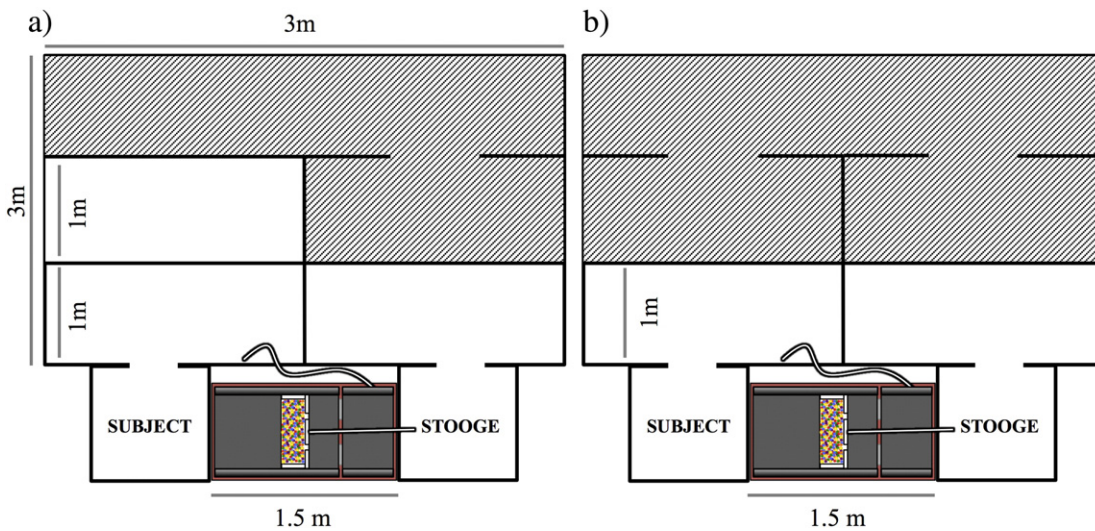
Fig. 2. Top view of the room arrangement in (a) No Audience, and (b) Audience conditions. Shading represents the areas of the habitat to which the social group has access during test sessions.

table in each condition before experiencing the Audience conditions (both as a subject and as an audience member).

2.4. Behavioral coding

All test sessions were videotaped and coded for pulling and scratching behavior. Pulling behavior (whether or not the subject collapsed the table within each 60 s trial) and the latency to pull (the amount of time elapsed from food loss until the table was collapsed) were coded from video by two independent coders who were blind to condition. Binary pulling behavior between coders was perfectly correlated (Pearson's $r(40) = 1.00$); pulling latencies were in agreement between coders (Pearson's $r(116) = 0.92$).

The frequency of scratching behavior was coded from video by two independent coders who were also blind to condition. For this purpose, the video for each trial was clipped to begin once the food tray was flush with the stooge's testing enclosure (thus removing evidence of the means by which the tray was moved) and the audio track was removed to eliminate identifying audio (i.e. experimenter clarification of trial or reference to testing date). Scratching bouts were coded as periods when the subject's digits made repetitive, deliberate contact with his/her body. Instances in which monkeys scratched distinctly different parts of the body with the same hand or switched hands mid-bout were classified as separate bouts. Inter-coder reliability was 0.908 (Pearson's r) for the presence (yes/no) of scratching behavior and 0.896 (Pearson's r) for the frequency of scratching bouts on a trial-by-trial basis.

2.5. Data analysis

We conducted generalized linear mixed models in the R (R Core Team, 2014) package *lme4* (Bates, 2010). In particular, we used the glmer function to examine monkeys' propensity to collapse the table as a binary outcome with a logit link function, building models based on maximum likelihood. These models therefore accounted for correlation in responses due to repeated trials within subjects (Baayen, 2008). We conducted post-hoc tests in the R package *multcomp* (Hothorn, Bretz, & Westfall, 2008) using the glht function. In addition to the main analyses that examined whether scratching predicted pulling behavior, we also assessed whether monkeys scratched at different rates across contexts. Like the main analyses of pulling, we analyzed scratching using GLMMs with the lme4 package, but here we used a Poisson link function to analyze the count of total scratching bouts in

each trial as the dependent variable. We then compared model fits using likelihood ratio tests (LRT) (Bolker et al., 2008).

3. Results

Overall, monkeys collapsed the table on $25.7\% \pm 3.7$ (Mean $\pm$ SE) of trials in the Partner Feeding condition, $20.1\% \pm 3.4$ of trials in the Outcome Disparity condition, $26.4\% \pm 3.7$ of trials after Theft, but only $9.0\% \pm 2.4$ of trials in the Loss condition (Fig. 3a). To analyze pulling behavior, we first built a basic model including *subject* as random factor (random subject intercepts); *trial number* as a covariate to assess learning effects within sessions; and each individual's *pretest pulling frequency* (in the Pretest's Other-Feeding trials) as a covariate to account for individual differences in propensity to collapse the table. Our basic model revealed that trial number was not a significant predictor, indicating that pulling propensity did not shift over trials within a given session. However, individuals who collapsed the table more in the Pretest's Other-Feeding trials collapsed the table more in test sessions ($p < 0.05$). In a second model, we then added *condition* as an additional predictor to test whether the stooge's intention and the inequity of the resource distribution influenced the monkeys' responses. In fact, including condition increased model fit, compared to the basic model ($\chi^2 = 23.56$, $df = 3$, $p < 0.001$). In particular, post-hoc pairwise comparisons revealed that performance in the Loss condition significantly differed from the other conditions ($p < 0.05$ for significant parameter comparisons): monkeys were more likely to collapse the table when the stooge had access to the food, compared to when the food was simply out of the subject's reach. The third model including *scratching* did not improve model fit (LRT: $\chi^2 = 1.05$, $df = 1$, $p = 0.31$, n.s.), however. As discussed in the next section, while capuchins exhibited differential scratching behavior across conditions, they collapsed the table at similar rates regardless of their arousal ($18.3\% \pm 2.7$ of trials with scratching, and $21.4\% \pm 2.1$ without; see Fig. 3b). Lastly, the full model added *audience* as a factor (see Table 1 for parameters of the full model) but this did not improve model fit compared to the condition-only model ($\chi^2 = 2.78$, $df = 2$, $p = 0.41$, n.s.). In fact, capuchins collapsed the table at nearly identical, rates regardless of audience condition: on $22.4\% \pm 3.0$ of trials with an audience and $19.3\% \pm 2.0$ of trials without an audience (Fig. 3c).

Overall, these findings highlight that the major predictor of whether the capuchins collapsed the table was whether their partner had access to the desirable food resource—regardless of how the conspecific acquired the food, whether the subject was emotionally aroused, and whether others were proximate to the interaction. As an additional
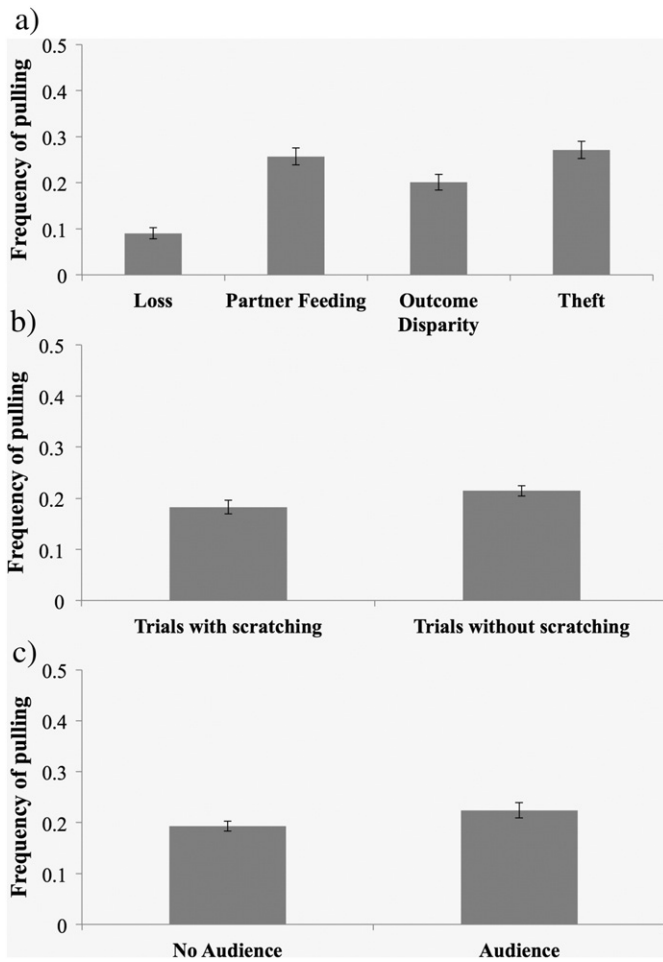
Fig. 3. Punishment across context. (a) Frequency of punishment by condition. (b) Frequency of punishment on trials with/without scratching. (c) Frequency of punishment in No Audience/Audience conditions. Error bars represent standard error.

check on these results, we then examined the monkey's latency to collapse the table across conditions. We found that monkeys collapsed the table after an average of 27.6 ± 17.7 s. However, a repeated-measures ANOVA revealed that there was no effect of either condition (F = 1.148, df = 3, $p = 0.398$) or presence of an audience (F = 0.776, df = 1, $p = 0.931$) on subjects' latency to collapse the table. This indicates that monkeys responded to food loss events with similar rapidity across contexts. This supports the conclusion that neither the cause of the food loss nor the presence a social audience impacted monkeys' decisions to punish.

Importantly, we did find that capuchins showed evidence of differential emotional reactivity to these situations, as indexed by

Table 1
Factors influencing capuchins' likelihood to collapse the table (Full Model).

Factor		Estimate	S.E.	Z	p
Trial	Covariate	−0.021	0.052	−0.399	0.690
Pretest	Covariate	−0.502	0.231	−2.176	<0.05
Scratching	Covariate	−0.128	0.146	−0.876	0.381
Audience	Baseline: No Audience	0.218	0.252	0.866	0.387
Condition	Outcome Disparity v. Loss	1.121	0.391	2.864	<0.05
	Partner Feeding v. Loss	1.571	0.387	4.061	<0.001
	Theft v. Loss	1.580	0.384	4.110	<0.001
	Partner Feeding v. Outcome Disparity	0.450	0.323	1.391	0.454
	Theft v. Outcome Disparity	0.459	0.320	1.435	0.454
	Theft v. Partner Feeding	0.009	0.310	0.030	0.976

their rates of scratching across conditions. The monkeys' differential rates of scratching indicates that they did detect differences between punishment conditions as well the presence of the audience, even though this information did not impact their punishment decisions. Specifically, monkeys engaged in more scratching bouts when the stooge had sole access to the food resource (Partner Feeding: Mean ± SE = 0.79 ± 0.10 bouts per trial), compared to conditions in which subjects initially had access to the food before losing it (Loss: 0.55 ± 0.07; Outcome Disparity: 0.49 ± 0.7, Theft: 0.43 ± 0.06; see Fig. 4a). To analyze these data, we first built a basic model that included *subject* as a random factor, and *trial* as a covariate to account for any changes in scratching over a test session. Our basic model revealed that trial number was not a significant predictor, however. In a second model, we then added *condition* as a predictor, which increased model fit ($\chi^2 = 17.48$, df = 3, p < 0.001). Pair-wise comparisons revealed that monkeys engaged in significantly more scratching bouts in the Partner Feeding condition compared to all other conditions (p < 0.05 for significant comparisons)—suggesting that capuchins were most aroused in this context. Finally, the full model including the presence of an audience further improved model fit (LRT: $\chi^2 = 12.41$, df = 1, p < 0.001), suggesting that subjects were, in some way, sensitive to the audience manipulation, as they scratched more in the no audience condition than they did in the audience condition. In fact, capuchins engaged in an average of 0.41 ± 0.06 scratching bouts per trial when an audience was present and 0.64 ± 0.05 bouts per trial in the absence of an audience (Fig. 4b; see Table 2 for parameters from the full model). Although we did not initially predict this pattern of performance, this finding is consistent with evidence that some wild-living capuchin monkeys show increases in scratching behavior when distanced from their social group (Polizzi di Sorrentino et al., 2012).

Taken together, these results indicate that the main factor driving subjects' punishment was the presence of the stooge eating the high-value resource. In our models of the capuchins' pulling behavior, the main predictor of whether the monkeys collapsed the table was condition. In particular, monkeys collapsed the table more whenever the conspecific was eating the food, regardless of how she obtained it. This response was not due to mere frustration at viewing inaccessible food, as monkeys were less likely to collapse the table when the resource was out of reach and no other monkey could access it. The results from the Pretest confirm that subjects understood the basic setup: individuals never collapsed the table when they had access to the food, but did when a partner was feeding from the tray. Moreover, the importance of conditions as a predictor held even though our models accounted for other potential motivators of the capuchins' behavior, such as individual differences in propensity to collapse the table. Yet other potentially important motivators of punishment – the intention of the conspecific, the emotional arousal of the actor, and the presence of a social audience – did not impact the monkeys' decisions to punish. Importantly, our analysis of the capuchins' scratching behaviors indicates that capuchins were differentially aroused by the different social conditions—and were in fact sensitive to the audience manipulation. However, this sensitivity did not translate into any differences in their actual punishment responses.

4. Discussion

To goal of this study was to investigate the roots of human-like punitive behaviors in another highly cooperative primate species. Our findings indicate that our capuchin monkeys were most likely to pursue punitive measures when confronted with a conspecific possessing relatively more of a food resource, regardless of how this situation arose. Importantly, punishment was not the result of mere frustration over an inaccessible resource, as monkeys were significantly less likely to collapse the table when no conspecific was eating from it. This suggests that the presence of another monkey with access to the resource was what drove their punitive behavior. Additionally, unlike punishment
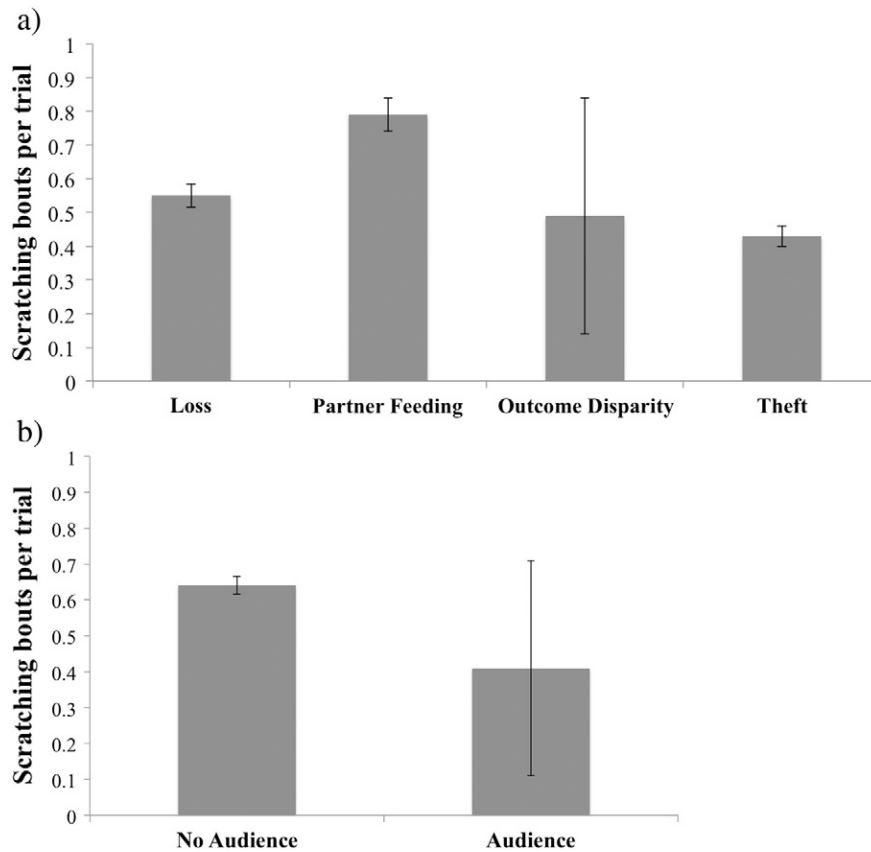
Fig. 4. Scratching bouts across context. (a) Mean scratching bouts per trial by condition. (b) Mean scratching bouts per trial in No Audience/Audience conditions. Error bars represent standard error.

in chimpanzees (Jensen et al., 2007), our data suggest that capuchin punishment does not seem to be the product of increased emotional arousal. While monkeys showed differential scratching across social contexts, their arousal level was not predictive of their tendency to collapse the table. This pattern of performance suggests that punishment in monkeys arises exclusively when monkeys can directly impact another individual who is benefitting from access to the resource.

Our findings demonstrate important similarities as well differences between the motivators of punishment of humans and capuchin monkeys. In terms of commonalities, both capuchins and humans appear to attend to relative resource distribution when making decisions about punishing others. Our results show that our capuchins specifically pursue punitive measures when they are confronted with a conspecific possessing relatively more of a food resource. Like humans (e.g., Houser & Xiao, 2010; Johnson et al., 2009; Raihani & McAuliffe, 2012), capuchins therefore punish more when they have relatively less than another individual. However, unlike humans, capuchin monkeys do not appear to account for how such inequity emerged. In contrast to human adults (e.g., Charness & Levine, 2003; Falk et al., 2008), children

(e.g., Cushman et al., 2013), and chimpanzees (Jensen et al., 2007), our capuchins fail to take intentionality into account when making punitive decisions. Specifically, capuchins punished at equal rates when the conspecific intentionally caused an unequal distribution and when the conspecific merely benefitted from an unequal distribution. Although previous work suggests that this species takes intentional actions into account in other contexts (e.g., Drayton & Santos, 2014; Phillips et al., 2009), this ability to discriminate intentional from unintentional actions does not feed into the capuchins' decisions to undertake punitive actions in the current study.

Capuchin punishment also does not appear to be driven by increased negative emotion. Unlike in both chimpanzees (Jensen et al., 2007) and adult humans (Pillutla & Murnighan, 1996; Xiao & Houser, 2005), negative emotional arousal in capuchin monkeys is not predictive of increased engagement in punishment behavior—despite differences in scratching behavior indicating emotional arousal across social contexts within our testing paradigm. This suggests that punishment in our capuchin monkeys is not simply the physical manifestation of emotional arousal; rather, punishment in capuchin monkeys appears to be systematically directed toward the individual benefitting from unequal access to a desirable resource. Indeed, our data suggest that capuchins may not account for the sorts of reputational cues that influence human punishment behavior (Kurzban et al., 2007). Specifically, we found that the presence of an audience did not impact capuchin punishment in our task, even though capuchins are known to show audience effects in other contexts (de Waal et al., 2008; Pollick et al., 2005).

Given that capuchins attended solely to disadvantageous resource distributions when punishing in our task, our findings present a pattern of capuchin punishment behavior consistent with two distinct (but not mutually exclusive) psychological explanations: capuchins may punish because they are *inequity averse* or because they are feeling *spiteful*. Inequity aversion involves a predisposition for equitable outcomes

Table 2
Factors influencing frequency of capuchins' scratching bouts (Full Model).

Factor		Estimate	S.E.	Z	p
Trial	Covariate	−0.014	0.024	−0.589	0.556
Audience	Baseline: No Audience	−0.440	0.129	−3.414	<0.001
Condition	Outcome Disparity v. Loss	−0.099	0.163	−0.603	0.868
	Partner Feeding v. Loss	0.366	0.147	2.496	0.050
	Theft v. Loss	−0.234	0.170	−1.381	0.501
	Partner Feeding v. Outcome Disparity	0.465	0.151	3.080	<0.050
	Theft v. Outcome Disparity	−0.136	0.173	−0.783	0.868
	Theft v. Partner Feeding	−0.600	0.157	−3.812	<0.001

often expressed by disapproval or avoidance of situations producing inequality, and may have co-evolved alongside cooperative abilities (Brosnan, 2011). Consistent with an aversion to inequity, monkeys in the current study reliably punished a conspecific in possession of more food. Previous work has shown that capuchins respond negatively to cases of disadvantageous inequity (see review in Brosnan, 2011), and thus one possibility is that similar psychological motivations are at play in this species' punishment decisions. More specifically, subjects might punish because of a psychological motivation to reduce inequity by equating the difference between their resources (nothing) and the stooge's resources by eliminating her access to the food.

Our results could also be explained by a different psychological motivation: spite. While biologists typically define spite as taking an action at cost to oneself to impose a cost on another, spite at the psychological level involves a tendency to inflict suffering upon a target as a means to an end (e.g., Jensen, 2010). Although spite is typically considered unique to human cooperation (Jensen, 2010), the current results are consistent with the possibility that capuchins may experience spite at the psychological level as well. We found that monkeys punished the stooge by collapsing the table even though doing so provided no potential benefit for them and imposed a (small) energetic cost. This sort of costly engagement in punitive actions without potential future benefit possesses many characteristics consistent with both biological and psychological definitions of spite. It is important to note, however, that the current study cannot assess the ultimate (e.g., evolutionary) consequences of the monkeys' behavioral tendencies in the context of natural social interactions. While monkeys' propensity to collapse the table appears spiteful in the short term, it remains an open question whether this propensity would generally result in long-term costs to the monkeys in accordance with traditional biological definitions of spite. Indeed, it is possible that these sorts of responses accrue benefits in the monkeys' normal social interactions: such punishment behaviors might alter the future behavior of conspecifics such that they would be less likely to interfere with future feeding bouts. Ultimately, this would be a beneficial outcome, given that capuchins can face high levels of competition for resources with groupmates when foraging in the wild (Janson, 1985).

Overall, our results show that capuchins engage in second-party punishment, but their decisions are motivated by factors different from those underlying such punishment in other non-human species (Jensen et al., 2007). While chimpanzees selectively collapsed the table more often when another conspecific had stolen the food – a behavior correlated with increased emotional arousal – we found that capuchins' behavior was driven by social comparisons of access to a valuable resource. The importance of both sensitivity to inequity and spite in models of human cooperation suggests that capuchins may also exhibit these patterns due to their sophisticated cooperative abilities. As a result, it appears as though the evolutionary roots of some human-like punitive tendencies may extend even deeper than previously thought.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2015.12.002.

Acknowledgments

References

Abbink, K., & Herrmann, B. (2011). The moral costs of nastiness. *Economic Inquiry*, 49(2), 631–633. http://dx.doi.org/10.1111/j.1465-7295.2010.00309.x.

Abbink, K., & Sadrieh, A. (2009). The pleasure of being nasty. *Economics Letters*, 105, 306–308. http://dx.doi.org/10.1016/j.econlet.2009.08.024.

Anderson, J. R., Takimoto, A., Kuroshima, H., & Fujita, K. (2013). Capuchin monkeys judge third-party reciprocity. *Cognition*, 127, 140–146.

Aureli, F., Cozzolinot, R., Cordischif, C., Cozzolino, R., Cordischi, C., & Scucchi, S. (1992). Kin-oriented redirection among Japanese macaques: An expression of a revenge system? *Animal Behaviour*, 44, 283–291. http://dx.doi.org/10.1016/0003-3472(92)90034-7.

Baayen, R. H. (2008). *Analyzing linguistic data. A practical introduction to statistics.* Cambridge, MA: Cambridge University Press.

Bates, D. (2010). lme4 package: Linear mixed-effects models using S4 classes. [Internet]. Available from: http:// www.R-project.org

Beersma, B., & Van Kleef, G. A. (2011). How the grapevine keeps you in line: Gossip increases contributions to the group. *Social Psychological and Personality Science*, 2(6), 642–649. http://dx.doi.org/10.1177/1948550611405073.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2008). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution*, 24, e127–e135.

Bone, J. E., & Raihani, N. J. (2015). Human punishment is motivated by both a desire for revenge and a desire for equality. *Evolution and Human Behavior*, 36, 323–330. http://dx.doi.org/10.1016/j.evolhumbehav.2015.02.002.

Boyd, R., Gintis, H., & Bowles, S. (2010). Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science*, 328(617), 617–620. http://dx.doi.org/10.1126/science.1183665.

Boyd, R., Gintis, H., Bowles, S., & Richerson, P. J. (2003). The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences U S A*, 100(6), 3531–3535. http://dx.doi.org/10.1073/pnas.0630443100.

Brosnan, S. F. (2010). What do capuchin monkeys tell us about cooperation? In D. R. Forsythe, & C. L. Hoyt (Eds.), *For the greater good of all: Perspectives on individualism, society, & leadership. Jepson series on leadership studies* (pp. 11–28). Palgrave Macmillan Publishers.

Brosnan, S. F. (2011). A hypothesis of the co-evolution of cooperation and responses to inequity. *Frontiers in Neuroscience*, 5(43), 1–12. http://dx.doi.org/10.3389/fnins.2011.00043.

Brosnan, S. F., Freeman, C., & De Waal, F. (2006). Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. *American Journal of Primatology*, 68(7), 713–724. http://dx.doi.org/10.1002/ajp.20261.

Buckholtz, J. W., & Marois, R. (2012). The roots of modern justice: Cognitive and neural foundations of social norms and their enforcement. *Nature Neuroscience*, 15(5), 655–661.

Call, J., Hare, B., Carpenter, M., & Tomasello, M. (2004). "Unwilling" versus "unable": Chimpanzees' understanding of human intentional action. *Developmental Science*, 7(4), 488–498. http://dx.doi.org/10.1111/j.1467-7687.2004.00368.x.

Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*, 12(5), 187–192. http://dx.doi.org/10.1016/j.tics.2008.02.010.

Charness, G., & Levine, D. I. (2003). The road to hell: An experimental study of intentions. *Department of Economics, UCSB*.

Clutton-Brock, T. H., & Parker, G. A. (1995). Punishment in animal societies. *Nature*. http://dx.doi.org/10.1038/373209a0.

Cota-McKinley, A. L., Woody, W. D., & Bell, P. A. (2001). Vengeance: Effects of gender, age, and religious background. *Aggressive Behavior*, 27, 343–350. http://dx.doi.org/10.1002/ab.1019.

Crofoot, M. C., & Wrangham, R. W. (2010). Intergroup aggression in primates and humans: The case for a unified theory. *Mind the gap* (pp. 171–195). Berlin Heidelberg: Springer.

Cushman, F., Sheketoff, R., Wharton, S., & Carey, S. (2013). The development of intent-based moral judgement. *Cognition*, 127, 6–21.

de Waal, F. B. M. (1982). *Chimpanzee politics: Power and sex among apes.* London, UK: Jonathan Cape.

de Waal, F. B. M., & Davis, J. M. (2003). Capuchin cognitive ecology: Cooperation based on projected returns. *Neuropsychologia*, 41(2), 221–228. http://dx.doi.org/10.1016/S0028-3932(02)00152-5.

de Waal, F. B. M., Leimgruber, K. L., & Greenberg, A. R. (2008). Giving is self-rewarding for monkeys. *Proceedings of the National Academy of Sciences U S A*, 105(36), 13685–13689. http://dx.doi.org/10.1073/pnas.0807060105.

de Waal, F. B. M., & Suchak, M. (2010). Prosocial primates: Selfish and unselfish motivations. *Philosophical Transactions of the Royal Society of London B*, 365, 2711–2722. http://dx.doi.org/10.1098/rstb.2010.0119.

Drayton, L. A., & Santos, L. R. (2014). Capuchins' (*Cebus apella*) sensitivity to others' goal-directed actions in a helping context. *Animal Cognition*, 17, 689–700. http://dx.doi.org/10.1007/s10071-013-0700-5.

Ellingsen, T., & Johannesson, M. (2008). Anticipated verbal feedback induces altruistic behavior. *Evolution and Human Behavior*, 29, 100–105. http://dx.doi.org/10.1016/j.evolhumbehav.2007.11.001.

Engelmann, J. M., Herrmann, E., & Tomasello, M. (2012). Five-year olds, but not chimpanzees, attempt to manage their reputations. *PloS One*, 7(10), e48433. http://dx.doi.org/10.1371/journal.pone.0048433.

Falk, A., Fehr, E., & Fischbacher, U. (2008). Testing theories of fairness—Intentions matter. *Games and Economic Behavior*, 62(1), 287–303. http://dx.doi.org/10.1016/j.geb.2007.06.001.

Fehr, E., & Fischbacher, U. (2004). Social norms and human cooperation. *Trends in Cognitive Sciences*, 8(4), 185–190. http://dx.doi.org/10.1016/j.tics.2004.02.007.

Fehr, E., & Gächter, S. (2000). Fairness and retaliation: The economics of reciprocity. *Journal of Economic Perspectives*, 14(3), 159–182. http://dx.doi.org/10.1257/jep.14.3.159.

Fehr, E., & Gächter, S. (2002). Altruistic punishment in humans. *Nature, 415*, 137–140. http://dx.doi.org/10.1038/415137a.

Fehr, E., & Schmidt, K. M. (1999). A theory of fairness, competition, and cooperation. *Quarterly Journal of Economics, 114*, 817–868 (Retrieved from: http://www.jstor.org/stable/2586885).

Gintis, H., Smith, E. A., & Bowles, S. (2001). Costly signaling and cooperation. *Journal of Theoretical Biology, 213*, 103–119. http://dx.doi.org/10.1006/jtbi.2001.2406.

Gürerk, O., Irlenbusch, B., & Rockenbach, B. (2006). The competitive advantage of sanctioning institutions. *Science, 312*(108), 108–111. http://dx.doi.org/10.1126/science.1123633.

Hamlin, J. K. (2013). Moral judgment and action in preverbal infants and toddlers: Evidence for an innate moral core. *Current Directions in Psychological Science, 22*(3), 186–193. http://dx.doi.org/10.1177/0963721412470687.

Hamlin, J. K., & Wynn, K. (2011). Young infants prefer prosocial to antisocial others. *Cognitive Development, 26*(1), 30–39. http://dx.doi.org/10.1016/j.cogdev.2010.09.001.

Hattori, Y., Kuroshima, H., & Fujita, K. (2005). Cooperative problem solving by tufted capuchin monkeys (*Cebus apella*): Spontaneous division of labor, communication, and reciprocal altruism. *Journal of Comparative Psychology, 119*, 335–342.

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences, 108*, 13847–13851.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal, 50*(3), 346–363.

Houser, D., & Xiao, E. (2010). Inequality-seeking punishment. *Economics Letters, 109*, 20–23.

Janson, C. (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology & Sociobiology, 18*, 125–138.

Jensen, K. (2010). Punishment and spite, the dark side of cooperation. *Philosophical Transactions of the Royal Society B, 365*, 2635–2650.

Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are vengeful but not spiteful. *Proceedings of the National Academy of Sciences, 104*, 13046–13050.

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. http://dx.doi.org/10.1098/rspb.2005.3417.

Johnson, T., Dawes, C. T., Fowler, J. H., McElreath, R., & Smirnov, O. (2009). The role of egalitarian motives in altruistic punishment. *Economics Letters, 102*, 192–194. http://dx.doi.org/10.1016/j.econlet.2009.01.003.

Kenward, B., & Dahl, M. (2011). Preschoolers distribute scarce resources according to the moral valance of recipients' previous actions. *Developmental Psychology, 47*, 1054–1064.

Kurzban, R., DeScioli, P., & O'Brien, E. (2007). Audience effects on moralistic punishment. *Evolution and Human Behavior, 28*, 75–84. http://dx.doi.org/10.1016/j.evolhumbehav.2006.06.001.

Lakshminarayanan, V. R., & Santos, L. R. (2008). Capuchin monkeys are sensitive to others' welfare. *Current Biology, 18*, R999–R1000.

Leimgruber, K. L., Shaw, A., Santos, L. R., & Olson, K. R. (2012). Young children are more generous when others are aware of their actions. *PloS One, 7*(10), e48292. http://dx.doi.org/10.1371/journal.pone.0048292.

Maestripieri, D., Schino, G., Aureli, F., & Toisi, A. (1992). A modest proposal: Displacement activities as an indicator of emotions in primates. *Animal Behavior, 44*, 967–979.

McAuliffe, K., Blake, P. R., Kim, G., Wrangham, R. W., & Warneken, F. (2013). Social influences on inequity aversion in children. *PloS One, 8*(12), e80966. http://dx.doi.org/10.1371/journal.pone.0080966.

McAuliffe, K., Blake, P. R., & Warneken, F. (2014). Children reject inequity out of spite. *Biology Letters, 10*, 20140743. http://dx.doi.org/10.1098/rsbl.2014.0743.

McAuliffe, K., Jordan, J. J., & Warneken, F. (2015). Costly third-party punishment in young children. *Cognition, 134*, 1–10. http://dx.doi.org/10.1016/j.cognition.2014.08.013.

Melis, A. P., & Tomasello, M. (2013). Chimpanzees' (*Pan troglodytes*) strategic helping in a collaborative task. *Biology Letters, 9*, 20130009. http://dx.doi.org/10.1098/rsbl.2013.0009.

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*. http://dx.doi.org/10.1098/rspb.2010.1735.

Nelson, W. R. (2002). Equity or intention: It is the thought that counts. *Journal of Economic Behavior and Organization, 48*, 423–430. http://dx.doi.org/10.1016/S0167-2681(01)00245-1.

Phillips, W., Barnes, J. L., Mahajan, N., Yamaguchi, M., & Santos, L. R. (2009). 'Unwilling' versus 'unable': Capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science, 12*, 938–945.

Piazza, J., & Bering, J. M. (2008). Concerns about reputation via gossip promote generous allications in an allocation game. *Evolution and Human Behavior, 29*, 172–178.

Pillutla, M. M., & Murnighan, J. K. (1996). Unfairness, anger, and spite: Emotional rejections of ultimate offers. *Organizational Behavior and Human Decision Processes, 68*, 208–224.

Polizzi di Sorrentino, E., Schino, G., Tiddi, B., & Aureli, F. (2012). Scratching as a window into the emotional responses of wild tufted capuchin monkeys. *Ethology, 118*, 1072–1084. http://dx.doi.org/10.1111/eth.12008.

Pollick, A. S., Gouzoules, H., & de Waal, F. B. M. (2005). Audience effects on food calls in captive brown capuchin monkeys, *Cebus apella*. *Animal Behaviour, 70*, 1273–1281. http://dx.doi.org/10.1016/j.anbehav.2005.03.007.

R Core Team (2014). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing (URL http://www.R-project.org/).

Rabin, M. (1993). Incorporating fairness into game theory and economics. In C. F. Camerer, G. Loewenstein, & M. Rabin (Eds.), *Advances in behavioral economics* (pp. 297). Princeton, NJ: Princeton University Press (cited 2014 Apr. 18).

Raihani, N. J., & McAuliffe, K. (2012). Human punishment is motivated by inequity aversion, not a desire for reciprocity. *Biology Letters, 8*, 802–804. http://dx.doi.org/10.1098/rsbl.2012.0470.

Raihani, N. J., Thornton, A., & Bshary, R. (2012). Punishment and cooperation in nature. *Trends in Ecology and Evolution, 27*(5), 288–295. http://dx.doi.org/10.1016/j.tree.2011.12.004.

Riedl, K., Jensen, K., Call, J., & Tomasello, M. (2012). No third-party punishment in chimpanzees. *Proceedings of the National Academy of Sciences, 109*, 14824–14829.

Robbins, E., & Rochat, P. (2011). Emerging signs of strong reciprocity in human ontogeny. *Frontiers in Psychology, 2*, 1–14.

Shaw, A., Li, V., & Olson, K. R. (2013). Reputation is everything. *Navigating the Social World*, 220–224.

Sheskin, M., Bloom, P., & Wynn, K. (2014). Anti-equality: Social comparison in young children. *Cognition, 130*, 152–156. http://dx.doi.org/10.1016/j.cognition.2013.10.008.

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

Takimoto, A., Kuroshima, H., & Fujita, K. (2010). Capuchin monkeys (*Cebus apella*) are sensitive to others' reward: An experimental analysis of food-choice for conspecifics. *Animal Cognition, 13*, 249–261. http://dx.doi.org/10.1007/s10071-009-0262-8.

Vaish, A., Carpenter, M., & Tomasello, M. (2010). Young children selectively avoid helping people with harmful intentions. *Child Development, 81*(6), 1661–1669. http://dx.doi.org/10.1111/j.1467-8624.2010.01500.x.

Vaish, A., Missana, M., & Tomasello, M. (2011). Three-year-old children intervene in third-party moral transgressions. *The British Journal of Developmental Psychology, 29*(Pt 1), 124–130. http://dx.doi.org/10.1348/026151010X532888.

Vonk, J., Brosnan, S., Silk, J., Henrich, J., Richardson, A., Lambeth, S. P., Schapiro, S. J., & Povinelli, D. J. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behavior, 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*(7), 1414–1420. http://dx.doi.org/10.1371/journal.pbio.0050184.

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science, 311*(5765), 1301–1303. http://dx.doi.org/10.1126/science.1121448.

Xiao, E., & Houser, D. (2005). Emotion expression in human punishment behavior. *Proceedings of the National Academy of Sciences U S A, 102*(20), 7398–7401. http://dx.doi.org/10.1073/pnas.0502399102.