Preschool children and chimpanzees incur costs to watch punishment of antisocial others

Natacha Mendes¹, Nikolaus Steinbeis^{2,3,4*}, Nereida Bueno-Guerra^{5,6}, Josep Call^{5,7} and Tania Singer[©]

When misfortune befalls another, humans may feel distress, leading to a motivation to escape. When such misfortune is perceived as justified, however, it may be experienced as rewarding and lead to motivation to witness the misfortune. We explored when in human ontogeny such a motivation emerges and whether the motivation is shared by chimpanzees. Chimpanzees and four- to six-year-old children learned through direct interaction that an agent was either prosocial or antisocial and later saw each agent's punishment. They were given the option to invest physical effort (chimpanzees) or monetary units (children) to continue watching. Chimpanzees and six-year-olds showed a preference for watching punishment of the antisocial agent. An additional control experiment in chimpanzees suggests that these results cannot be attributed to more generic factors such as scene coherence or informational value seeking. This indicates that both six-year-olds and chimpanzees have a motivation to watch deserved punishment enacted.

ow cooperation in societies can emerge and be maintained remains an evolutionary puzzle1-5. Punishment of antisocial group members is arguably one key mechanism capable of ensuring that levels of cooperation remain high in human⁶ as well as other species^{7,8}. It has been shown that the experience of emotions is a likely proximate cause that sustains cooperation and motivates costly punishment of antisocial others in humans^{4,9-11}. Seeing others suffer can induce emotional states such as empathic distress¹² or concern¹³, of which the latter is a powerful motivator for altruistic helping^{10,12,14}. Along with humans, several other animal species have been tested for reactions to witnessing pain in conspecifics^{15–24}, providing evidence for at least some forms of empathic responding. In humans, empathic reactions can be radically undermined and change to feelings of pleasure when the suffering victim was previously antisocial or perceived as an outgroup member^{10,11}. Such signals of reward are critical predictors of a subsequent absence of helping and desire for revenge and punishment^{10,11}. Thus, young human infants display an early preference for prosocial compared with antisocial agents^{25,26} and prefer those who are antisocial to previously antisocial others²⁷. Further, preschoolers have been shown to endorse the misfortune of competitors^{28,29}, to think antisocial others deserving of punishment³⁰ and to punish transgressions of outgroup members more than those of ingroup members³¹. Much less is known about how such mechanisms might operate in one of our closest living relatives, the chimpanzee (but see refs 32-35). Although chimpanzees seem to develop attitudes towards others based on previous prosocial and antisocial behaviours^{36–38}, nothing is known about the phylogenetic origins of the motivation to watch the enactment of revenge.

We used a cross-species forced-choice behavioural paradigm to study whether chimpanzees and children aged 4–6 years differentially incur costs to continue watching the punishment of agents (human agents for the chimpanzees, puppets for the children) depending on whether these agents had been prosocial or antisocial in a directly experienced previous interaction with them (Studies 1 and 2). The prosocial or antisocial nature of the agents was operationalized by means of them offering valuable goods to children (their favourite toys) and chimpanzees (food). Whereas the prosocial agent would both offer and give the goods to the participant, the antisocial agent would offer the goods first but then withdraw them. The punishment procedure for all the studies entailed a punisher applying physical punishment by hitting each of the two agents (either prosocial or antisocial; Fig. 1a,b). Crucially, after a brief period of witnessing the punishment, this was rendered invisible to subjects (that is, it occurred in another part of the room for chimpanzees or was hidden by a puppet-theatre curtain for children). Therefore, to continue watching the punishment, subjects had to incur costs, which for chimpanzees entailed the physical effort of operating a heavy sliding door to get to the invisible part of the room (Fig. 1a) and for children entailed paying tokens or monetary units (henceforth MUs) for the curtain of the puppet theatre to be raised again (Fig. 1b). As indicators of a motivation to witness punishment, we used the amount of cost incurred to continue watching the punishment. We operationalized cost incurred as the expenditure of MUs for children and of physical energy and time for chimpanzees. We predicted that both chimpanzees (Study 1) and children (Study 2) would be more motivated to watch the punishment of the antisocial agent than of the prosocial agent. For the children, we also predicted signs of greater positive emotions during the initial punishment of the antisocial agent compared with the prosocial agent. To measure emotional correlates, we scored facial expressions (for example smiles or frowns) during the punishment of the two agents. In chimpanzees, no predictions for specific positive emotions were made, given that happy or positive emotional signs in chimpanzees are rarely observed, except in playful activities in which the ape performs play panting (laughter-like) vocalizations on being physically touched (tickled/chased)³⁹.

¹Max Planck Institute for Human Cognitive and Brain Sciences, Research Group Neuroanatomy and Connectivity, Leipzig, Germany. ¹Department of Social Neuroscience, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. ³Institute of Psychology, Leiden University, Leiden, The Netherlands. ⁴Department of Clinical, Educational and Health Psychology, University College London, London, UK. ⁵Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. ⁵Department of Psychology and Clinical Psychobiology, University of Barcelona, Barcelona, Spain. ⁵School of Psychology and Neuroscience, University of St Andrews, St Andrews, Scotland, UK. Natacha Mendes and Nikolaus Steinbeis contributed equally to this work. *e-mail: n.steinbeis@ucl.ac.uk

ARTICLES NATURE HUMAN BEHAVIOUR

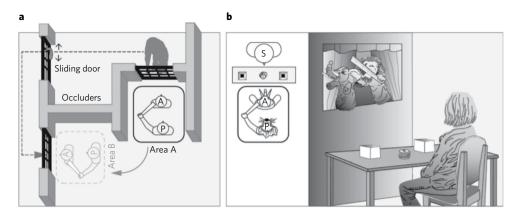


Fig. 1 [Experimental design for chimpanzees and children. Subjects (S) watch the punishment of an agent (A), who was previously either prosocial or antisocial, by a punisher (P). **a**, For the chimpanzees in the visible conditions, the punishment took place outside the cage of the chimpanzee. For the invisible conditions, the punishment moved to a part of the room out of sight from the chimpanzee. **b**, For the children, the punishment was visible until a curtain fell, and children were asked to put their MUs into the box on the right to continue watching the punishment.

We were also interested in whether, in line with previous work in humans¹¹, there were signs of empathic distress when witnessing prosocial agents being punished. In children, there is a wealth of evidence for such basic empathic tendencies when watching others harm themselves40,41, as expressed by verbalizations and facial expressions such as frowns42. Thus, we predicted that children would show greater signs of empathic distress (increased frowns) in response to the punishment of the prosocial compared with the antisocial agent. Whether chimpanzees display empathic tendencies in such situations is much less known. One key behavioural indicator of empathic distress is whether individuals have a motivation to escape the distressing situation¹⁴. Chimpanzees approach victims of aggression, and they direct agonistic behaviour towards aggressors and/or affiliative behaviour towards victims²⁰. We were therefore interested in whether the punishment of the prosocial agent would elicit escape behaviour (by operating the heavy sliding door and moving into another part of the room without visual access to the punishment of the agent) or approach behaviour (by remaining in the room during the punishment). For chimpanzees, we also used their vocalizations (defined here as a compound of distress and display vocalizations; see Methods section) during the initial punishment as indicators of emotional arousal. The vocalizations were categorized according to their acoustic and temporal properties⁴³ and grouped according to the call categories suggested by Goodall⁴⁴.

We performed an additional study with chimpanzees (Study 3) to control for the possibility that incurring a cost to watch an antisocial agent being punished merely indicates that this is seen as more socially informative or more coherent with the flow of the preceding events. Study 3 was identical to that of Study 1, with the single difference that in Study 3 chimpanzees did not directly experience but merely witnessed how the prosocial and the antisocial agents interacted with another chimpanzee (stooge). If chimpanzees preferentially watch the punishment of antisocial agents as a function of these more superficial aspects rather than their motivational substrate, the pattern of results should be the same in both studies. Based on previous studies showing that chimpanzees do not punish others who stole food from third parties $^{38,45}\,\mathrm{but}$ that they preferentially beg for food from those who were prosocial to others^{37,46}, we predicted that chimpanzees in Study 3, unlike Study 1, would not care to watch or vocalize differentially when others (regardless of whether they were prosocial or antisocial) were being punished. Note that Study 3 differed from Study 1 only in terms of the extent to which the chimpanzee subjects were directly affected by the agents' behaviour, while keeping all other aspects of the experimental set-up constant.

It is important to note that our dependent behavioural variable of opening the heavy sliding door for the chimpanzees is the same throughout all conditions. However, we interpret it differently depending on the condition (that is, to continue witnessing the punishment when it is invisible or to escape into another room when it is visible; see Discussion section for details).

Although we tested three age groups of children, we were agnostic to any age-related changes in our variables of interest. Given our a priori predictions, one-tailed statistics were applied for the factor prosociality. All other comparisons were two-tailed. Thus, for the chimpanzees (Studies 1 and 3), this resulted in a 2×2 factorial design with factor prosociality (prosocial/antisocial) and visibility (visible/invisible) and one trial for each condition. For children (Study 2), this resulted in a design with one factor of prosociality (prosocial/antisocial) and with four trials for each condition.

Results

Study 1: Chimpanzees following directly experienced pro- and antisocial behaviour. Chimpanzees differentially operated the heavy sliding door depending on whether punishment was visible and whether the agent had been previously prosocial towards them (Cochran's Q=8.59, degrees of freedom, d.f. = 3, P=0.043, N=16). We conducted pair-wise follow-up comparisons between the two invisible conditions to test our hypothesis of increased motivation to witness the punishment of an agent who had been previously antisocial towards the subject. Subjects were significantly more likely to incur the physical costs of opening the heavy metal door in the antisocial invisible condition (50% of the subjects) than in the prosocial invisible condition (18.75% of the subjects) (sign test: P = 0.032, N=16, one-tailed; Fig. 2a). We conducted another pair-wise followup comparison between the two visible conditions to test for the behavioural effects of empathic distress (that is, increased opening of the door to move to another room when the punishment of the prosocial agent was visible to the subject). Here we found no significant difference in the number of subjects who opened the door during the prosocial visible condition compared with the antisocial visible condition (sign test: P = 0.313, N = 16, one-tailed; Fig. 2a).

To assess the presence of vocalizations associated with emotional arousal during the punishment of either of the agents, the testing event was divided into three periods: an initial baseline in which just the agent was present; a pre-hit period where the punisher appeared but had not started to punish the agent; and a first-hit period during which the punishment took place. We looked at these periods separately for each of the two agents. There was a significant difference between the three periods in the duration of the vocalizations in

NATURE HUMAN BEHAVIOUR ARTICLES

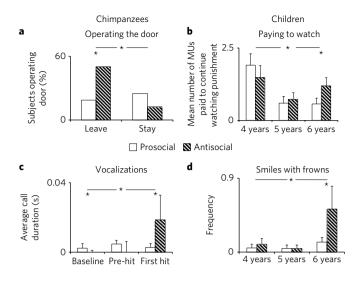


Fig. 2 | Behavioural data and emotional indicators for chimpanzees (Study 1; *N* = 17) and children (Study 2; *N* = 65). **a**, More chimpanzees opened the heavy sliding door to continue watching the punishment in the invisible antisocial condition than in the invisible prosocial condition. Not all the chimpanzees opened the door. 'Leave' indicates that the punisher and punished agent left to move to an invisible part of the room. 'Stay' indicates that punisher and punished agents remained visible. **b**, All children paid to continue watching some of the punishment, but only six-year-old children paid more to watch the antisocial agent being punished compared with the prosocial agent. **c**, Chimpanzees expressed greater distress vocalizations when watching the punishment of the prosocial human agent. **d**, Only six-year-old children displayed more frequent smiles coupled with frowns during the punishment of the antisocial compared with the prosocial agent. The error bars show s.e.m. The asterisk indicates significant differences (*P* < 0.05).

the presence of the prosocial agent (Friedman exact test: F=9.82, P=0.004, N=16; Fig. 2c), but we found no such difference in the presence of the antisocial agent (F=4.67, P=0.107, N=16; Fig. 2c). Comparing the vocalizations in response to the presence and punishment of the prosocial and the antisocial agents showed that chimpanzees produced longer vocalizations in the baseline period when facing the antisocial agent compared with the prosocial one (Wilcoxon exact test: $T^+=21$, P=0.031, $N_{\text{total}}=16$; corrected for the duration of each period in the punishment phase: that is, baseline, pre-hit, hit periods) and longer vocalizations when the prosocial agent was being punished than when the antisocial agent was being punished in the hit period (Wilcoxon exact test: $T^+=21$, P=0.031, $N_{\text{total}}=16$; Fig. 2c).

To assess whether the prosocial/antisocial exposure procedure had been effective, we assessed the subjects' preference for the prosocial and antisocial agent upon completion of the tasks (see Methods section). This was tested by allowing the chimpanzees to beg for food from the two agents. Chimpanzees showed no preference for requesting food from the prosocial over the antisocial agent (Wilcoxon signed rank test: T^+ = 89, N = 17, P = 0.579).

Finally, we also assessed relationships between the chimpanzees' vocalizations and their behaviour. We found that chimpanzees who produced vocalizations during the punishment of the prosocial agent were more likely to open the door to continue witnessing punishment of the antisocial agent than those who did not produce any vocalizations (57% versus 12.5%; chi-squared test: $\chi^2 = 5.402$, P = 0.041). This suggests that those chimpanzees who signal distress in response to a prosocial agent's punishment are also more motivated to observe deserved punishment being enacted.

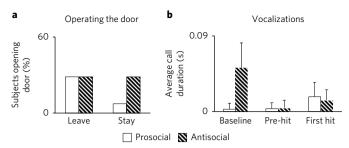


Fig. 3 | Behavioural data and emotional indicators for chimpanzees in Study 3 (*N* = 14). a,b, There were no differences in the chimpanzees' behaviour (a) or vocalizations (b) between any of the conditions. The error bars show s.e.m.

Study 2: Children. To test for the hypothesis that children would show an increased motivation to observe the punishment of a previously antisocial agent, we compared the number of MUs spent on continuing to watch the punishment of the prosocial and the antisocial agents. The data were normally distributed and met assumptions for parametric tests. A repeated measures ANOVA with agent as a within-subject and age-group as a between-subject factor indicated a significant interaction between the factors agent and age-group in how MUs were allocated to watch the punishment $(F_{(2.62)} = 3.417; P = 0.039, Fig. 2b)$. Thus, only 6-year-olds allocated more MUs to watch the punishment of the antisocial compared with the prosocial agent ($F_{(1,20)}$ =12.246; P=0.002; for 4-year-olds and 5-year-olds P > 0.2; Fig. 2b). Although there was a linear increase in comprehension of the task with age ($F_{(2,62)}$ =5.26; P=0.007), this did not correlate with MUs allocated for watching punishment of either the prosocial or the antisocial agent (all values of r < 0.2; P > 0.1).

Coding of facial expressions while watching the initial round of punishment showed significant age-differences in number of smiles co-occurring with frowns depending on which agent was being punished ($F_{(1,62)}$ =2.294; P=0.03, one-tailed; Fig. 2d). Thus, only 6-year-olds showed an increased mixture of positive and negative emotions (facial expressions) while watching the punishment of the antisocial compared with the prosocial agent ($F_{(1,20)}$ =3.155; F=0.045, one-tailed; Fig. 2d). We assessed the number of frowns during the initial round of punishment as an indication of empathic distress in the children at seeing the punishment of the agents. Whereas children frowned for both the prosocial (one-sample t-test: $t_{(64)}$ =2.408; F=0.019) and the antisocial agent (one-sample t-test: $t_{(64)}$ =2.644; t=0.010), this did not differ between the two agents. Frowning during the punishment did not interact further with age (P>0.4).

To test the children for a preference for either of the two agents, children were asked explicitly on completion of the task which of the two agents they (1) considered nicer, (2) would be more willing to share with and (iii) would prefer to play with (see Methods and Supplementary Information). Children of all three age groups displayed a clear preference for the prosocial over the antisocial agent (paired t-test: $t_{(64)} = 4.279$; P < 0.001) with no age differences in this preference (one-way ANOVA; P > 0.607).

Study 3: Chimpanzees following indirectly experienced proand antisocial behaviour. This study was conducted to rule out potential alternative explanations for the outcome of Study 1, including an increased social informational value in seeing antisocial others receive punishment or finding it more coherent in terms of the unfolding of events. Unlike Study 1, we found no evidence that chimpanzees differentially opened the heavy sliding door in the four conditions (Cochran's Q=3, d.f. = 3, P=0.484, N=14; Fig. 3a).

ARTICLES NATURE HUMAN BEHAVIOUR

We also analysed the presence of vocalizations associated with emotional arousal during the punishment of each of the agents during the baseline, pre-hit and first-hit periods. There was no significant difference between the three periods in the duration of the vocalizations in the presence of the prosocial and antisocial agents (prosocial, Friedman exact test: F=0.125, P=1.00, N=14; antisocial, F=3.26, P=0.218, N=14; Fig. 3b).

We used a paradigm previously shown to capture preferences of pro-over antisocial agents in chimpanzees³⁷ to test for this in the present study. We found that chimpanzees begged significantly more often from the prosocial than the antisocial agent (frequency of begs corrected for the amount of time spent in front of the correspondent agent, Wilcoxon signed rank test: $T^+ = 82$, $N_{\text{total}} = 14$, P = 0.008).

Discussion

Our findings demonstrate that chimpanzees and 6-year-old children, but not 4-year-old and 5-year old children, possess greater motivation to watch the punishment of others whom they had previously experienced as antisocial towards themselves as compared with prosocial agents. Thus, chimpanzees endured greater physical efforts, and 6-year-old children spent more MUs, to continue watching the punishment of an agent who had previously withheld something valuable from the subjects than to watch the punishment of someone who had been prosocial and shared the valuable items. In contrast, chimpanzees spent the same effort to continue watching the punishment of a human agent regardless of the agents' social behaviour towards other chimpanzees.

We observed concomitant indicators of affective responses in the children. Six-year-old children showed a greater mixture of positive and negative emotions in response to watching the punishment of the antisocial agent than they did for the prosocial one. The combination of these emotions, rejoicing in the misfortune of a disliked other, is also known as Schadenfreude⁴⁷. These data suggest that in children, pleasure at seeing deserved punishment may be linked to the increased costs incurred to continue watching it. Recent studies have shown that differential punishment of selfish behaviours of in-group and out-group members already occurs from 6 years onwards⁴⁸ and that around 6 years, children are capable of experiencing such potentially conflicting emotions⁴⁹. Thus, 6 years of age may be a critical developmental time point at which children are willing to sacrifice their resources to see fairness enacted⁵⁰. Importantly, even though there were some age differences in the comprehension of the experimental procedure, comprehension scores did not correlate with our behavioural measure, suggesting that differences in comprehension cannot account for the age-related effect in the MUs expended. Further, our MUs were made meaningful to children through a subsequent exchange for stickers, which have been shown to be valuable items for the youngest as well as the oldest children of our age groups⁵¹⁻⁵⁴.

Previous studies have shown that chimpanzees engage in punishment of conspecifics who had previously stolen their food by causing the thief's food to disappear^{38,45}. Study 1 demonstrates that also in the absence of food, chimpanzees are motivated to watch antisocial agents being punished after directly experiencing the antisocial behaviour themselves. One could argue that the chimpanzees' reaction could be driven by emotional engagement. However, chimpanzees were more aroused when they watched the punishment of the prosocial agent. Following indirectly experienced prosocial and antisocial behaviour, chimpanzees were equally motivated to watch punishment of the prosocial and the antisocial agents. This is consistent with findings showing that chimpanzees do not punish those who stole food from third parties⁴⁵. The results from Study 3, in which chimpanzees merely observed the prosocial and antisocial interaction prior to the agents' punishment, help us to interpret the results from Study 1. In both

studies, all basic elements were kept constant except for the degree of the chimpanzee's involvement. Thus, alternative explanations such as increased social informational value or a greater coherence in the unfolding of the scene can be ruled out. Instead, the most likely interpretation is that chimpanzees have an increased motivation to observe such punishment because it follows a desirable action towards someone who behaved antisocially towards them. The literature contains many examples of animals willing to incur energy costs for something they find rewarding^{55–57}. It is therefore tempting to argue that watching antisocial others being harmed is rewarding and pleasurable to chimpanzees. Also suggestive of an emotional antecedent to such behaviour is the finding that chimpanzees who had vocalized distress during the punishment of the prosocial agent were also more likely to incur a cost to continue witnessing the deserved punishment of an antisocial other. Thus, when punishment is deserved, the experience of distress is abolished, leading chimpanzees to actively seek to observe such punishment. However, in the absence of direct evidence, we remain cautious about positing the presence of actual positive emotions as a driver for the observed behaviour.

In addition to signs of Schadenfreude in children, we found evidence of empathic distress across all three age groups. However, this was not modulated by whether the agent had been previously prosocial or antisocial towards them. Even though children as young as 3 years old have been shown to differentiate their empathic helping between previously prosocial and antisocial others^{58,59}, and all age groups showed a preference for the prosocial agent, no difference in empathic responding could be found. Chimpanzees produced longer vocalizations indicative of emotional arousal during the punishment of the prosocial agent that had directly interacted with them, but no differential vocalizations occurred when they witnessed the agent being punished following the indirectly experienced prosocial and antisocial behaviour. Even though in chimpanzees it is difficult to label the valence of such vocalizations as they can reflect conflicting emotions⁴⁴, the specificity of their occurrence (longer vocalizations during the hitting of the prosocial agent compared with the antisocial agent) suggests that they might reflect something akin to empathic distress. However, chimpanzees did not signal distress by attempting to escape witnessing the punishment of the prosocial agent, nor did they try to approach and console the victim of the aggression as suggested by observational studies²⁰. These conflicting results (distress vocalizations versus non-escape/non-approach behaviour) make it difficult to pinpoint the underlying motivation of the chimpanzees' behaviours upon witnessing the punishment of the prosocial agent.

There are some limitations to the present studies. One is the fact that interactions were observed between individuals that were not of the same species as the subject. However, this concern is reduced given that both chimpanzees and 6-year-olds responded differentially to the two agents. Although such cross-species set-ups are common in the study of social behaviour of both human and nonhuman primates⁶⁰⁻⁶², future work will need to assess how far these findings extend to interactions with one's own species. Furthermore, the different dependent variables for the chimpanzees and the children (physical energy versus MUs) make direct interspecies comparisons difficult. Although using different dependent variables has the advantage of optimizing procedures for each species, thus avoiding potential biases favouring one of the species, future work may seek to expand the findings using the same dependent variables for greater comparability. Finally, we were unable to counterbalance the administration of the direct and indirect exposures to the prosocial and antisocial in chimpanzees. Our results, however, were consistent with the existing literature on the occurrence of punishment following directly and indirectly experienced transgressions in chimpanzees, which ameliorates to some extent the concerns derived from our current design.

NATURE HUMAN BEHAVIOUR ARTICLES

We studied the evolutionary and ontogenetic origins of an increased motivation to watch the punishment of antisocial others. By incurring costs, chimpanzees and 6-year-old children showed greater motivation to continue watching the punishment of an antisocial over a prosocial agent. Furthermore, children displayed differential responses of mixed positive and negative emotions when they witnessed punishment of antisocial agents, which suggest that they might take some form of pleasure from this. Although such a mechanism is still uncertain in chimpanzees, vocalizations of emotional arousal produced when they witnessed the suffering of a prosocial agent, and their absence when witnessing the suffering of an antisocial agent, might indicate that affective responses such as pleasure constitute an important motivational contributor to the exaction of revenge, with early evolutionary origins. Crucially, chimpanzees did not vocalize differentially nor incur differential costs to witness the punishment when seeing the two agents punished following indirectly experienced prosocial and antisocial behaviour. These findings provide evidence for the evolutionary origins of an increased motivation to watch punishment of antisocial behaviour with—at least in children—possible links to feelings of pleasure underlying such a motivation. Such a motivation seems to develop at a protracted rate, similar to higher-level cognitive skills⁶³, and might emerge at an age at which children begin to care so much for justice that they are willing to pay for it.

Methods

Ethics statement. The studies reported in this manuscript were approved by the local ethics committee of the University of Leipzig and complied with all relevant regulations. Thus, the ethics committee of the University of Leipzig approved the study (Ethics Approval Number: 367-11-26092011). Caregivers provided a written consent form to use the acquired data. Additionally, the chimpanzee work was approved by the MPI-EVA—Zoo Leipzig ethical committee.

Participants. Studies 1 and 3. In Study 1, we tested 17 chimpanzees (Pan troglodytes). There were 5 males ranging in age between 8 and 38 years (M=16 years and 8 months) and 12 females ranging in age between 8 and 37 years (M=22 years and 5 months). In Study 3, we tested 14 chimpanzees. There were 5 males ranging in age between 8 and 38 years (M=15 years and 10 months) and 9 females ranging in age between 12 and 42 years (M=27 years and 3 months). All chimpanzees were housed at the Wolfgang Koehler Primate Research Center, Leipzig Zoo, Germany. Eleven of them participated in both studies, whereas the rest could not do so because they were unavailable (see Supplementary Table 1 for rearing history and participation in each study). All indoor and outdoor enclosures were furnished with vegetation, climbing structures and visual barriers. Subjects were not deprived of food or water during the experiment.

Study 2. We tested 72 children. There were three age groups: 24 4-year-olds (M=4.15, age range 4.04-4.35 years), 24 5-year-olds (M=5.04, age range 4.97-5.4 years), and 24 6-year-olds (M=6.17, age range 5.98-6.33 years). In each group, there were equal numbers of boys and girls. Seven children had to be removed from the analyses because of procedural error or fussiness. All remaining subjects received all conditions. All children were recruited from a subject database at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany.

Experimental procedures. Studies 1 and 3. These two studies consisted of four phases: 'Training', 'Exposure', 'Preference' and 'Punishment' (actual test). Before entering the Punishment phase, chimpanzees received a sequence of training stages (see 'Training phase' in Supplementary Information) to ensure that they understood how to open the heavy mesh sliding door that would allow them access to the adjacent room. After the training, all subjects were exposed directly (Study 1) or indirectly (Study 3, by witnessing an interaction between a human agent and a conspecific 'stooge' chimpanzee) to two different human agents, one at a time. The agents acted either prosocially towards the subject/stooge (Study 1/Study 3), by providing food, or antisocially, by teasing and not allowing the subject/stooge to get access to the food (see 'Exposure phase' in Supplementary Information). Whether the agent was prosocial or antisocial was counterbalanced across subjects. To reduce carry-over effects between studies, different agents participated in Study 3 (except for the punisher), which was conducted a few months after Study 1. To test the efficacy of the 'Exposure phase', a 'Preference phase' was designed to test for preferential begging from the two agents (see Supplementary Information for more details). In the 'Punishment phase' (see Supplementary Information), either the prosocial or the antisocial agent entered the testing room and sat in front of the Plexiglas window in the subjects' room. After 5 seconds of being seated in front of

the Plexiglas window (henceforth referred to as baseline period), a second agent, the punisher, entered the room. The punisher approached the agent from behind with a human facial expression of rage (henceforth referred to as pre-hit period) and started beating her up (henceforth referred to as hit period) with a stick for 4 seconds (four hits with the stick, rate 1 Hz). While being beaten up, the agent cried out in pain. After the initial punishment period (4 seconds) the agent either remained in her initial position for the whole time of the punishment visible to the subject (10 more seconds, Fig. 1a), the so-called 'visible' condition; or left her initial position (area A, see Fig. 1a) and went into another area of the room invisible to the chimpanzee (area B, see Fig. 1a) where the punishment continued for 10 more seconds, so-called 'invisible' condition. If subjects wanted to continue watching the punishment in the invisible condition, they had to open the heavy sliding door (learned during the Training phase) and move in front of the Plexiglas window in the new room. Similarly, if they wanted to escape from the punishment in the visible condition happening in front of them, they had to operate the door to move to another part of the room where this would then be invisible (Fig. 1a).

All sessions were videotaped, and the following variables were coded from digital files: (1) opening of the heavy sliding door; (2) duration of the vocalizations associated with emotional arousal, namely screams, whimpers and worried hoots classified as distress vocalizations⁴³, and (waa) barks and (pant) hoots classified as display vocalizations⁴³. As previously mentioned, vocalizations were categorized according to their acoustic structure and temporal measures and grouped according to the call categories suggested in ref. ⁴⁴. Distress and display vocalizations were lumped together and the combined results used for statistical analysis. The duration of the calls was analysed with the sound analysis software Avisoft and Praat.

To assess inter-observer reliability, a second observer coded a random sample of 20% of the trials. Inter-observer reliability was high for opening the sliding door (Study 1: Pearson correlation r=1.000, P<0.001; Study 3: r=1.000, P<0.001), for duration of the vocalizations (Study 1, distress calls: r=1.000, P<0.001; display calls: r=0.900, P<0.001; Study 3, distress calls: r=1.000, P<0.001; display calls: r=1.000, P<0.001), and for frequency of begs corrected for the amount of time spent in front of the corresponding human agent (Study 1: r=0.999, P=0.028; Study 3: r=0.997, P=0.048).

Study 2. Children came into the laboratory accompanied by at least one parent. Parents had been instructed before on the phone to bring six of their child's favourite toys, without the child noticing. These were then taken by the experimenter and used in the two Exposure phases. Children were given an initial endowment of four MUs. It was made clear that at the end of the experiment each of the MUs could be traded for one sticker.

This study consisted of four phases: 'Training,' Exposure' and 'Punishment' (actual test) and 'Preference'. In the Training phase, the experimental procedure was demonstrated using a miniature-sized puppet theatre. Following the Training phase, each child was exposed consecutively to two different puppets, a prosocial and an antisocial puppet (see 'Exposure phase' in Supplementary Information). Exposure entailed one of two puppets either acting prosocially by returning three of the child's favourite toys, or antisocially, by keeping them for itself. The puppets would bring up a toy from behind the theatre and hold it up to the child. After telling the child that it wanted to play with them, the prosocial puppet would hold the toy towards the child and put it into the child's hands, whereas the antisocial puppet would withdraw as soon as the child reached for the toy. Similar procedures have been shown to elicit clear preferences in infants⁶⁴. Which puppet was prosocial or antisocial was counterbalanced across subjects. Exposure and testing was performed for both puppets and fully counterbalanced across all subjects.

During the Punishment phase, the puppet to which children had just been exposed remained on stage. After 5 seconds, another (punisher) puppet appeared (different from the two agents), carrying a long stick. The punisher started beating the other (prosocial/antisocial) puppet with the stick for 5 seconds (five hits, rate 1 Hz). After the initial punishment period (5 seconds), the theatre curtain closed, rendering both the punisher and the punished puppet invisible. The punisher puppet then returned and said to the child that they were going to continue hitting the other puppet and that if the child would like to continue watching, then he or she should put one MU into a box to the right of the stage, whereas if the child did not want to continue watching, he or she should put a MU into a box to the left of the stage. Depending on where the children placed their MU, the curtains were drawn again or not, and children could continue observing the punishment or not. If they chose not to witness the punishment, the punishment was still executed behind closed curtains. If children decided not to continue watching on the first round, then the punisher puppet did not ask again whether the child cared for another round of witnessing punishment. However, if children decided to continue watching, the punisher asked again after 5 seconds of punishment if they would like to continue watching. Given that children had received four MUs, the maximum number of paid punishments was four. Thus, all subjects received exposure to the first round of punishment and the first question of whether they would like to continue watching. Depending on whether children paid for punishment, they were asked again until they either decided to stop watching or until they had no more MUs. The final round was the pursuit and punishment behind the curtain; thus the child continued to hear the puppet crying for 10 seconds longer but without visual access to the punishment.

ARTICLES NATURE HUMAN BEHAVIOUR

All sessions were videotaped, and the following variables were coded from digital files during the exposure phase as well as the punishment phase: (1) behaviours and verbalizations; (2) pure smiles, pure frowns and, given the potential ambivalence of seeing someone antisocial experience punishment, smiles occurring jointly with frowns. Two observers coded all the videos using the Interact software.

To assess inter-observer reliability, ratings were correlated. Inter-observer reliability was high for answering the questions of the punisher (r=0.99, P<0.0001) as well as for occurrence of smiles, frowns and smiles with frowns during the exposure as well as the punishment phase (all r>0.504, all P<0.0001).

At the end of the entire Punishment phase, the experimenter showed the two agents to the child and asked which puppet the child would rather play with, would rather give a sticker to, and thought was nicer. From this, a composite score of preference was obtained (see Supplementary Information).

All data were analysed in SPSS 23 (SPSS Statistics Software, IBM). No attempts to replicate the findings reported in this paper have been made.

Life Sciences Reporting Summary. Further information on experimental design is available in the Life Sciences Reporting Summary.

Data availability. The data that support the findings of this study are available from the corresponding author on reasonable request.

Received: 21 March 2017; Accepted: 9 November 2017; Published online: 18 December 2017

References

- Nowak, M. A. Five rules for the evolution of cooperation. Science 314, 1560–1563 (2006).
- Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity. Nature 437, 1291–1298 (2005).
- Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. The evolution of altruistic punishment. Proc. Natl Acad. Sci. USA 100, 3531–3535 (2003).
- Fehr, E. & Gächter, S. Altruistic punishment in humans. Nature 415, 137–140 (2002).
- Henrich, N. & Henrich, J. P. Why Humans Cooperate: A Cultural and Evolutionary Explanation (Oxford Univ. Press, Oxford, 2007).
- Henrich, J. & Boyd, R. Why people punish defectors: weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. J. Theor. Biol. 208, 79–89 (2001).
- Clutton-Brock, T. H. & Parker, G. A. Punishment in animal societies. *Nature* 373, 209–216 (1995).
- Hauser, M. D. Costs of deception: cheaters are punished in rhesus monkeys (Macaca mulatta). Proc. Natl Acad. Sci. USA 89, 12137–12139 (1992).
- De Quervain, D. J., Fischbacher, U., Treyer, V. & Schellhammer, M. The neural basis of altruistic punishment. Science 305, 1254–1258 (2004).
- Hein, G., Silani, G., Preuschoff, K., Batson, C. D. & Singer, T. Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. *Neuron* 68, 149–160 (2010).
- 11. Singer, T. et al. Empathic neural responses are modulated by the perceived fairness of others. *Nature* **439**, 466–469 (2006).
- 12. Batson, C. D. *The Altruism Question: Toward a Social-Psychological Answer* (Erlbaum, Hillsdale, NJ, 1991).
- Singer, T. et al. Empathy for pain involves the affective but not sensory components of pain. Science 303, 1157–1162 (2004).
- 14. Batson, C. D., Duncan, B. D., Ackerman, P., Buckley, T. & Birch, K. Is empathic emotion a source of altruistic motivation? *J. Pers. Soc. Psychol.* **40**, 290, 302 (1981)
- Cools, A. K., Van Hout, A. J. M. & Nelissen, M. H. Canine reconciliation and third-party-initiated postconflict affiliation: do peacemaking social mechanisms in dogs rival those of higher primates? *Ethology* 114, 53–63 (2008).
- Palagi, E. & Cordoni, G. Postconflict third-party affiliation in *Canis lupus*: do wolves share similarities with the great apes? *Animal Behav.* 78, 979–986 (2009).
- Seed, A. M., Clayton, N. S. & Emery, N. J. Postconflict third-party affiliation in rooks, Corvus frugilegus. Current Biol. 17, 152–158 (2007).
- Byrne, R. et al. Do elephants show empathy? J. Conscious. Stud. 15, 204–225 (2008).
- 19. Clay, Z. & de Waal, F. B. Bonobos respond to distress in others: consolation across the age spectrum. *PLoS One* **8**, e55206 (2013).
- Romero, T. & de Waal, F. Chimpanzee (Pan troglodytes) consolation: third-party identity as a window on possible function. J. Comp. Psychol. 124, 278 (2010).
- Mallavarapu, S., Stoinski, T., Bloomsmith, M. & Maple, T. Postconflict behavior in captive western lowland gorillas (*Gorilla gorilla gorilla*). Am. J. Primatol. 68, 789–801 (2006).
- Langford, D. J. et al. Social modulation of pain as evidence for empathy in mice. Science 312, 1967–1970 (2006).

- Bartal, I. B.-A., Decety, J. & Mason, P. Empathy and pro-social behavior in rats. Science 334, 1427–1430 (2011).
- Burkett, J. P. et al. Oxytocin-dependent consolation behavior in rodents. Science 351, 375–378 (2016).
- Hamlin, J. K., Wynn, K. & Bloom, P. Social evaluation by preverbal infants. Nature 450, 557–559 (2007).
- Hamlin, J. K. & Wynn, K. Young infants prefer prosocial to antisocial others. Cogn. Dev. 26, 30–39 (2011).
- Hamlin, J. K., Wynn, K., Bloom, P. & Mahajan, N. How infants and toddlers react to antisocial others. Proc. Natl Acad. Sci. USA 108, 19931–19936 (2011).
- Schulz, K., Rudolph, A., Tscharaktschiew, N. & Rudolph, U. Daniel has fallen into a muddy puddle—Schadenfreude or sympathy? *Br. J. Dev. Psychol.* 31, 363–378 (2013).
- Shamay-Tsoory, S. G., Ahronberg-Kirschenbaum, D. & Bauminger-Zviely, N.
 There is no joy like malicious joy: Schadenfreude in young children. *PloS ONE* 9, e100233 (2014).
- Tisak, M. S. Preschool children's judgments of moral and personal events involving physical harm and property damage. *Merrill-Palmer Q.* 39, 375–390 (1993).
- Jordan, J. J., McAuliffe, K. & Warneken, F. Development of in-group favoritism in children's third-party punishment of selfishness. *Proc. Natl Acad.* Sci. USA 111, 12710–12715 (2014).
- 32. De Waal, F. B. Good Natured (Harvard Univ. Press, London, 1996).
- De Waal, F. B. & Luttrell, L. M. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethol. Sociobiol.* 9, 101–118 (1988).
- 34. Jensen, K., Call, J. & Tomasello, M. Chimpanzees are rational maximizers in an ultimatum game. *Science* **318**, 107–109 (2007).
- Suchak, M. et al. How chimpanzees cooperate in a competitive world. Proc. Natl Acad. Sci. USA 113, 10215–10220 (2016).
- Herrmann, E., Keupp, S., Hare, B., Vaish, A. & Tomasello, M. Direct and indirect reputation formation in nonhuman great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*) and human children (*Homo sapiens*). *J. Comp. Psychol.* 127, 63–75 (2013).
- Russell, Y. I., Call, J. & Dunbar, R. I. Image scoring in great apes. Behav. Processes 78, 108–111 (2008).
- Jensen, K., Call, J. & Tomasello, M. Chimpanzees are vengeful but not spiteful. Proc. Natl Acad. Sci. USA 104, 13046–13050 (2007).
- Matsusaka, T. When does play panting occur during social play in wild chimpanzees? *Primates* 45, 221–229 (2004).
- Fabes, R. A., Eisenberg, N. & Eisenbud, L. Behavioral and physiological correlates of children's reactions to others in distress. *Dev. Psychol.* 29, 655–663 (1993).
- Eisenberg, N. et al. The relations of children's dispositional empathy-related responding to their emotionality, regulation, and social functioning. *Dev. Psychol.* 32, 195–209 (1996).
- Valiente, C. et al. Prediction of children's empathy-related responding from their effortful control and parents' expressivity. Dev. Psychol. 40, 911–926 (2004).
- Nishida, T., Zamma, K., Matsusaka, T., Inaba, A. & McGrew, W. C. Chimpanzee Behavior in the Wild: An Audio-Visual Encyclopedia (Springer Science & Business Media, Tokyo, 2010).
- 44. Goodall, J. The Chimpanzees of Gombe: Patterns of Behavior (Belknap, Cambridge, MA, 1986).
- Riedl, K., Jensen, K., Call, J. & Tomasello, M. No third-party punishment in chimpanzees. Proc. Natl Acad. Sci. USA 109, 14824–14829 (2012).
- Anderson, J. R., Takimoto, A., Kuroshima, H. & Fujita, K. Capuchin monkeys judge third-party reciprocity. Cognition 127, 140–146 (2013).
- 47. Smith, R. H. et al. Envy and Schadenfreude. Pers. Soc. Psychol. Bull. 22, 158-168 (1996).
- 48. Jordan, J. J., McAuliffe, K. & Warneken, F. Development of in-group favoritism in children's third-party punishment of selfishness. *Proc. Natl Acad. Sci. USA* 111, 12710–12715 (2014).
- Steinbeis, N. & Singer, T. The effects of social comparison on social emotions and behavior during childhood: the ontogeny of envy and Schadenfreude predicts developmental changes in equity-related decisions. *J. Exp. Child Psychol.* 115, 198–209 (2013).
- 50. McAuliffe, K., Jordan, J. J. & Warneken, F. Costly third-party punishment in young children. *Cognition* **134**, 1–10 (2015).
- Engelmann, J. M., Over, H., Herrmann, E. & Tomasello, M. Young children care more about their reputation with ingroup members and potential reciprocators. *Dev. Sci.* 16, 952–958 (2013).
- Blake, P. R., Piovesan, M., Montinari, N., Warneken, F. & Gino, F. Prosocial norms in the classroom: the role of self-regulation in following norms of giving. *J. Econ. Behav. Organ.* 115, 18–29 (2015).
- Smith, C. E., Blake, P. R. & Harris, P. L. I should but I won't: why young children endorse norms of fair sharing but do not follow them. *PloS ONE* 8, e59510 (2013).
- Dunfield, K., Kuhlmeier, V. A., O'Connell, L. & Kelley, E. Examining the diversity of prosocial behavior: helping, sharing, and comforting in infancy. *Infancy* 16, 227–247 (2011).

NATURE HUMAN BEHAVIOUR ARTICLES

- Salamone, J. D., Correa, M., Farrar, A. & Mingote, S. M. Effort-related functions of nucleus accumbens dopamine and associated forebrain circuits. *Psychopharmacology* 191, 461–482 (2007).
- Grossbard, C. L. & Mazur, J. E. A comparison of delays and ratio requirements in self-control choice. J. Exp. Anal. Behav. 45, 305–315 (1986).
- Beran, M. J. & Evans, T. A. Delay of gratification by chimpanzees (*Pan troglodytes*) in working and waiting situations. *Behav. Processes* 80, 177–181 (2009).
- Eisenberg, N. et al. The relations of emotionality and regulation to dispositional and situational empathy-related responding. *J. Pers. Soc. Psychol.* 66, 776–797 (1994).
- Vaish, A., Carpenter, M. & Tomasello, M. Young children selectively avoid helping people with harmful intentions. *Child Dev.* 81, 1661–1669 (2010).
- Custance, D. M., Whiten, A. & Bard, K. A. Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes & Hayes (1952) revisited. *Behaviour* 132, 837–859 (1995).
- Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P. & Bard, K. A. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). J. Comp. Psychol. 110, 3–14 (1996).
- Call, J., Hare, B., Carpenter, M. & Tomasello, M. 'Unwilling'versus 'unable': chimpanzees' understanding of human intentional action. *Dev. Sci.* 7, 488–498 (2004).
- 63. Hanus, D., Mendes, N., Tennie, C. & Call, J. Comparing the performances of apes (Gorilla gorilla, Pan troglodytes, Pongo pygmaeus) and human children (Homo sapiens) in the floating peanut task. PloS ONE 6, e19555 (2011).
- Dunfield, K. A. & Kuhlmeier, V. A. Intention-mediated selective helping in infancy. Psychol. Sci. 21, 523–527 (2010).

Acknowledgements

We are grateful to M. Tomasello for early input into the study design and to M. Allritz, V. Ehrich, K. Esau, E. Felsche, J. Grossmann, S. Hunger, S. Lorenz, J. Steinhardt, K. Schumann, K. Waldherr and K. Wenig for helping with the training phase and data collection with the chimpanzees at the Wolfgang Köhler Primate Research Centre; to Y. Hejja-Brichard and K. Schumann for analysing the chimpanzee vocalizations,

K. Schumann for analysing part of the chimpanzee behavioural data, M. Neuschulz and A. Hutschenreiter for inter-rater reliability coding of the chimpanzee data, and to C. Brenner, K. Mueller, C. Hoecker and J. Buergel for the data collection with the children. We thank T. Gruber, C. Crockford and A. Kalan for help in identifying some of the chimpanzee vocalizations, A. Kalan for help with the software Avisoft and Praat, H. Grunert and R. Pieszek for their help in constructing the experimental apparatus, and the zookeepers at the Leipzig Zoo for their help with the chimpanzees. Salaries of N.S., N.M. and T.S., as well as testing of the children, were supported by a Max Planck budget granted to T.S. as director of the Department of Social Neuroscience. N.S. was supported by the European Research Council (European Research Council (ERC) grant agreement no. 715282, project DEVBRAINTRAIN), as well as a Jacobs Research Fellowship. J.C. was supported in part by the ERC (grant agreement no. 609819, project SOMICS). N.B.-G. was supported by an FPU scholarship from the Spanish Ministry of Education (ref. FPU12/00409). With the exception of the Max Planck Society, none of the funders played a role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Author contributions

N.M., N.S., J.C. and T.S. conceived and designed the experiments: N.B.-G., N.M. and N.S. performed the experiments. N.M. and N.S. analysed the data. N.B.-G., N.M., N.S., T.S. and J.C. interpreted data and wrote the paper. Funding was provided by J.C. and T.S.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41562-017-0264-5.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to N.S.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.