1	Preschool children and chimpanzees incur costs to watch punishment of antisocial
2	others
3	
4	
5	Natacha Mendes ^{1*} , Nikolaus Steinbeis ^{2,3,4*} , Nereida Bueno-Guerra ^{5,6} , Josep Call ^{5,7} , Tania Singer
6	2
7	
8	1 Max Planck Institute for Human Cognitive and Brain Sciences, Research Group
9	Neuroanatomy & Connectivity, Stephanstraße 1A, 04103 Leipzig
10 11	2 Max Planck Institute for Human Cognitive and Brain Sciences, Department of Social Neuroscience, Stephanstraße 1A, 04103 Leipzig
	3 Institute of Psychology, Leiden University, 2333 AK Leiden, The Netherlands
12	
13	4 University College London, Department of Clinical, Educatinal and Health Psychology, London WC1H OAP
14 15	
15	5 Max Planck Institute for Evolutionary Anthropology, Department of Developmental and
	Comparative Psychology, Deutscher Platz 6, 04103 Leipzig
17	6 University of Barcelona, Department of Psychology and Clinical Psychobiology, Passeig de
18	Vall d'Hebrón 171, 08035 Barcelona
19 20	7 University of St Andrews, School of Psychology and Neuroscience, St Andrews, Fife KY16
20	9JP
21	
22	* These authors contributed equally to the work
23	
24 25	Corresponding author
26	Nikolaus Steinbeis
20	University College London, Department of Clinical, Educational and Health Psychology, London
27	WC1H OAP
29	Email: n.steinbeis@ucl.ac.uk
30	
31	Word Count: 5695
32	
33	Keywords: prosocial, antisocial, motivation to watch deserved punishment, chimpanzees,
33 34	children

35 Abstract

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 a motivation to witness such misfortune. We explored when in human ontogeny such a motivation emerges and if such a motivation is shared by chimpanzees. Chimpanzees and 4-6 year old children learned through direct interaction that an agent was either prosocial or antisocial and later saw each agent's punishment with the option to invest physical effort (chimpanzees) or monetary units (children) to continue watching. Chimpanzees and 6-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 6-year-olds and chimpanzees have a motivation to watch deserved punishment enacted.

48 Word Count: 149

- ___

- _ -

How cooperation in societies can emerge and be maintained remains an evolutionary puzzle¹⁻⁵. 68 69 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 70 71 that the experience of emotions is a likely proximate cause that sustains cooperation and 72 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 73 74 motivator for altruistic helping^{10,12,14}. Along with humans, several other animal species have been tested for reactions to witnessing pain in conspecifics¹⁵⁻²⁴, providing some evidence for at 75 76 least some forms of empathic responding. It has been shown in humans that empathic reactions 77 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 have 78 been shown to be critical predictors of a subsequent absence of helping and desire for revenge 79 and punishment^{10,11}. Thus, young human infants display an early preference for prosocial 80 compared to antisocial agents^{25,26} and prefer those who are antisocial to previously antisocial 81 others²⁷. Further, preschoolers have been shown to endorse the misfortune of competitors^{28,29}. 82 to think antisocial others as deserving of punishment³⁰ and to punish transgressions of outgroup 83 members more than those of ingroup members³¹. Much less is known about how such 84 mechanisms might operate in one of our closest living relatives, the chimpanzee (but see ³²⁻³⁵). 85 While it is known that chimpanzees appear to develop attitudes towards others based on 86 previous pro- and antisocial behaviors³⁶⁻³⁸, nothing is known about the phylogenetic origins of 87 88 the motivation to watch the enactment of revenge.

89

90 We used a cross-species forced-choice behavioral paradigm to study whether chimpanzees and 91 children aged 4-6 years differentially incur costs to continue watching the punishment of agents 92 depending on whether these had been pro- or antisocial in a directly experienced previous 93 interaction with them (Studies 1 and 2). The pro- or antisocial nature of the agents was 94 operationalized by means of them offering valuable goods to children (i.e. their favorite toys) 95 and chimpanzees (i.e. food). Whereas the prosocial agent would both offer and give the goods 96 to the participant, the antisocial agent would offer the goods first but then withdraw the goods. 97 The punishment procedure for all the studies entailed a punisher applying physical punishment 98 in the form of hitting each of the two agents (i.e. either prosocial or antisocial; Figure 1A and 99 1B). Crucially, after a brief period of witnessing the punishment, this was rendered invisible to 100 subjects (i.e. occurred in another part of the room for chimpanzees / was occluded by a curtain 101 of a puppet theatre for children). Therefore to continue watching the punishment subjects had to

102 incur costs, which for chimpanzees entailed physical effort by operating a heavy sliding door to 103 get to the invisible part of the room (Figure 1A) and for children entailed paying tokens or 104 monetary units (henceforth MUs) for the curtain of the puppet theatre to be raised again (Figure 105 1B). As indicators of a motivation to witness punishment we used the amount of cost incurred to 106 continue watching the punishment. We operationalized cost incurred as the expenditure of 107 valuable monetary units (MUs) for children and physical energy and time for chimpanzees. We 108 predicted that both chimpanzees (Study 1) and children (Study 2) would be more motivated to 109 watch the punishment of the antisocial compared to the prosocial agent. We also predicted 110 signs of greater positive emotions during the initial punishment of the two antisocial agent 111 compared to the prosocial agent for the children. To measure emotional correlates, we scored 112 facial expressions (e.g., smiles, frowns) during the punishment of the two agents. In 113 chimpanzees no predictions for specific positive emotions were made given that happy/positive 114 emotions in chimpanzees are very rarely observed, except in playful activities in which the ape being physically touched (tickled/chased) performs play panting vocalizations (laughter-like)³⁹. 115

116

117 We were also interested in whether, in line with previous work in humans¹¹, there were signs of 118 empathic distress when witnessing prosocial agents being punished. In children, there is already a wealth of evidence for such basic empathic tendencies when watching others harm 119 themselves^{40,41}, as expressed by verbalizations and facial expressions such as frowns⁴². Thus, 120 121 for children we predicted that they would show greater signs of empathic distress (increased 122 frowns) in response to the punishment of the prosocial compared to the antisocial agent. 123 Whether chimpanzees display empathic tendencies in such situations is much less known. One 124 kev behavioral indicator of empathic distress is whether individuals have a motivation to escape 125 the distressing situation¹⁴. Chimpanzees approach victims of aggression and direct agonistic 126 behavior towards aggressors and/or affiliative behavior towards victims²⁰. We were therefore 127 interested in whether the punishment of the prosocial agent would elicit escape behavior (by 128 operating the heavy sliding door and moving into another part of the room without visual access 129 to the punishment of the agent) or approach behavior (i.e. by remaining in the room during the 130 punishment). For chimpanzees, we also used their vocalizations (here defined as a compound 131 of distress and display vocalizations. See Material and Methods section for more details) during 132 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 133 134 categories suggested by Goodall⁴⁴.

136 We performed an additional study with chimpanzees (Study 3) to control for the possibility that 137 incurring a cost to watch an antisocial agent being punished merely indicates that this is seen as 138 more socially informative or more consistent with the flow of the preceding events. The 139 execution of Study 3 was identical to that of Study 1, with the single difference that in Study 3 140 chimpanzees did not directly experience but merely witnessed, how the prosocial and the 141 antisocial agents interacted with another chimpanzee (stooge). If chimpanzees preferentially 142 watch the punishment of antisocial agents as a function of these more superficial aspects rather 143 than their motivational substrate (anger- and revenge-based vs. norm-based punishment), the 144 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} but they preferentially 145 beg for food from those who were prosocial to others^{37,46} we predicted that chimpanzees in 146 147 Study 3, unlike Study 1, would not care to watch or vocalize differentially when others 148 (regardless of whether they were prosocial or antisocial) were being punished. Note that Study 149 3 differed from Study 1 only in terms of the extent to which the chimpanzee subjects were 150 directly affected by the agents' behavior, while keeping all other aspects of the experimental set-151 up constant.

152

153 It is important to note that our dependent behavioral variable of opening the heavy sliding door 154 for the chimpanzees is always the same throughout all conditions. However, we interpret it 155 differently depending on the condition (i.e., to continue witnessing the punishment when it is 156 invisible or to escape into another room when it is visible; see Discussion section for more 157 details). While we tested three age groups of children, we were agnostic to any age-related 158 changes in our variables of interest. Given our a-priori predictions one-tailed statistics were 159 applied for the factor prosociality. All other comparisons were two-tailed. Thus, for the 160 chimpanzees (Studies 1 and 3) this resulted in a 2x2 factorial design with factor prosociality 161 (prosocial/antisocial) and visibility (visible/invisible) and one trial for each condition. For children 162 (Study 2) this resulted in a design with one factor of prosociality (prosocial/antisocial) and with 4 163 trials for each condition.

164

165 Results

Study 1: Chimpanzees, Watching punishment following directly experienced pro- and antisocialbehavior

168 Chimpanzees differentially operated the heavy sliding door depending on whether punishment 169 was visible or not and whether the agent had been previously prosocial towards them or not 170 (Cochran's Q = 8.59, df = 3, P = 0.043, N = 16). We conducted pair-wise follow-up comparisons 171 between the two invisible conditions to test our hypothesis of an increased motivation to witness 172 the punishment of an agent who had been previously antisocial towards the subject. Subjects 173 were significantly more likely to incur the physical costs to open the heavy metal door in the 174 antisocial invisible condition (50% of the subjects) compared to the prosocial invisible condition 175 (18.75% of the subjects) (Sign test: P = 0.032, N = 16, one-tailed; Figure 2A). We conducted 176 another pair-wise follow-up comparison between the two visible conditions to test for the 177 behavioral effects of empathic distress (i.e. increased opening of the door to move to another 178 room when the punishment of the prosocial agent is visible to the subject). Here we found no 179 significant difference in the number of subjects who opened the door during the prosocial visible 180 condition compared to the antisocial visible condition (Sign test: P = 0.313, N = 16, one-tailed; 181 Figure 2A).

182

183 To assess the presence of vocalizations associated with emotional arousal during the 184 punishment of either of the agents, the testing event was divided into three periods; an initial 185 baseline where just the agent was present; a pre-hit period where the punisher appeared but 186 had not started to punish the agent, and a first-hit period during which the punishment actually 187 took place. We looked at these periods separately for each of the two agents. There was a 188 significant difference between the three periods in the duration of the vocalizations in the 189 presence of the prosocial agent (Friedman exact test: F = 9.82, P = 0.004, N = 16; Figure 2C) 190 but we found no such difference in the presence of the antisocial agent (F = 4.67, P = 0.107, N191 = 16; Figure 2C). Comparing the vocalizations in response to the presence and punishment of 192 the prosocial and the antisocial agents, showed that chimpanzees produced longer 193 vocalizations in the baseline period when facing the antisocial agent compared to the prosocial 194 one (Wilcoxon exact test: $T^{\dagger} = 21$, P = 0.031, $N_{total} = 16$; corrected for the duration of each 195 period in the Punishment phase, i.e., baseline, pre-hit, hit periods) and longer vocalizations 196 when the prosocial agent was being punished compared to when the antisocial agent was being punished in the hit period (Wilcoxon exact test: $T^{+} = 21$, P = 0.031, $N_{total} = 16$; Figure 2C). 197

198

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 Materials and Methods section). This was tested by allowing the chimpanzees to beg for food from the two agents to assess whether they showed a preference for one of them. 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). This could have been the result of the close physical proximity of both agents, which might not have allowed for a clear dissociation of the subject's behavior.

207

Finally, we also assessed relationships between the chimpanzees' vocalizations and their behavior. 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% vs 12.5%; Chi-Square 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 deserve punishment being enacted.

215

216 Study 2: Children

217 To test for the hypothesis that children would show an increased motivation to observe the 218 punishment of a previously antisocial agent, we compared the number of MUs spent on 219 continuing to watch the punishment of the prosocial and the antisocial agents. The data were 220 normally distributed and met assumptions for parametric tests. A Repeated Measures ANOVA 221 with agent as a within-subject and age-group as a between-subject factor, indicated a significant 222 interaction between the factors agent and age-group in how MUs were allocated to watch the 223 punishment ($F_{(2,62)}$ = 3.417; P = 0.039, Figure 2B). Thus, only 6-year-olds allocated more MUs to 224 watch the punishment of the antisocial compared to the prosocial agent ($F_{(1,20)}$ = 12.246; P = 225 0.002; for 4- and 5-year olds p > 0.2; Figure 2B). While there was a linear increase in 226 comprehension of the task with age ($F_{(2,62)} = 5.26$; P = 0.007) this did not correlate with MUs 227 allocated either for watching punishment of the prosocial or the antisocial agent (all rs < 0.2; P > 228 0.1).

229

230 Coding of facial expressions while watching the initial round of punishment showed significant 231 age-differences in number of smiles co-occurring with frowns depending on which agent was 232 being punished ($F_{(1,62)}$ = 2.294; P = 0.03, one-tailed; Figure 2D). Thus, only 6-year-olds showed 233 an increased mixture of positive and negative emotions (facial expressions) while watching the 234 punishment of the antisocial compared to the prosocial agent ($F_{(1,20)} = 3.155$; P = 0.045, onetailed; Figure 2D). We assessed the number of frowns during the initial round of punishment as 235 236 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: $t_{(64)} = 2.408$; P = 0.019) and 237

- the antisocial agent (one-sample t-test: $t_{(64)} = 2.644$; P = 0.010), this did not differ between the two agents. Frowning during the punishment did not interact further with age (P > 0.4).
- 240

To test the children for a preference for either of the two agents, children were asked explicitly which of the two agents they i) considered nicer, ii) would be more willing to share with and iii) would prefer to play with (see Materials and Methods section and SI). 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).

247 Study 3: Chimpanzees, Watching punishment following indirectly experienced pro- and248 antisocial behavior

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, df = 3, P = 0.484, N = 14).

254

We also analyzed 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).

260

Russell and colleagues³⁷ showed that upon witnessing an interaction between a human beggar and either a nice or a nasty agent, chimpanzees showed a preference for the former. We used Russell et al.'s paradigm to test for a potential preference between the prosocial and the antisocial agent³⁷. 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).

267

268 Discussion

Our findings demonstrate that chimpanzees and 6-year old but not 4 and 5-year old children appear to possess a motivation to watch the punishment of others who they had previously experienced as antisocial towards themselves as compared to prosocial agents. Thus, chimpanzees endured greater physical efforts and 6-year-old children spent more valuable MUs to continue watching the punishment of an agent who had previously withheld something valuable from the subjects (i.e. food for the chimpanzees and favorite toys for the children) as compared to 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 behavior towards other chimpanzees.

278

279 We observed concomitant indicators of affective responses in the children. Six-year old children 280 showed a greater mixture of positive and negative emotions in response to watching the 281 punishment of the antisocial agent compared to the prosocial one. The combination of these 282 emotions, rejoicing in the misfortune of a disliked other, is also known as Schadenfreude⁴⁷. 283 These data suggest that in children, pleasure at seeing deserved punishment may be linked to 284 the increased costs incurred to continue watching it. Recent studies have shown that differential 285 punishment of selfish behaviors 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 286 287 conflicting emotions⁴⁹. Thus, 6 years of age may be a critical developmental time point at which children are willing to actually sacrifice their resources to see fairness enacted⁵⁰. Importantly, 288 289 even though there were some age differences in the comprehension of the experimental 290 procedure, comprehension scores did not correlate with our behavioral measure, suggesting 291 that any differences in comprehension cannot account for the age-related effect in the MUs 292 expended. Further, our MUs were made meaningful to children through a subsequent 293 conversion to stickers, which have been shown to be valuable items for the youngest as well as 294 the oldest children of our age groups⁵¹⁻⁵⁴.

295

296 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 297 298 that also in the absence of food, chimpanzees are motivated to watch antisocial agents being 299 punished after directly experiencing the antisocial behavior themselves. One could argue that 300 the chimpanzees' reaction could be driven by emotional engagement. However, chimpanzees 301 were more aroused when they watched the punishment of the prosocial agent. Following 302 indirectly experienced pro- and antisocial behavior, chimpanzees were equally motivated to 303 watch punishment of the pro- 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 304 305 Study 3, in which chimpanzees merely observed the prosocial and antisocial interaction prior to

306 the agents' punishment, help us to interpret the results from Study 1. In both studies all basic 307 elements were kept constant except for the degree of the chimpanzee's involvement. Thus, 308 alternative explanations such as increased social informational value or a greater coherence in 309 the unfolding of the scene can be ruled out. Instead, the most likely interpretation based on 310 these findings is that chimpanzees have an increased motivation to observe such punishment 311 because it follows a desirable action towards someone who behaved antisocially towards 312 themselves. The literature abounds with examples of animals willing to incur energy costs for something they find rewarding⁵⁵⁻⁵⁷. It is therefore tempting to argue that watching antisocial 313 others getting harmed is rewarding and pleasurable also to chimpanzees. Suggestive of an 314 315 emotional antecedent to such behavior is also the finding of individual differences in the 316 relationship between vocalizations and opening the door to witness punishment. Thus, 317 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 318 319 other. Thus, when punishment is deserved, the experience of distress is abolished leading 320 chimpanzees to actively seek out observing such punishment. However, in the absence of direct 321 evidence, we remain cautious with an account positing the presence of actual positive emotions 322 as a driver for the observed behavior.

323

324 In addition to signs of Schadenfreude in children, we found evidence of empathic distress 325 across all three age groups. However, this was not differentially modulated by whether the 326 agent had been previously prosocial or antisocial towards them. Even though children as young 327 as 3-year old have been shown to differentiate their empathic helping between previously prosocial and antisocial others^{58,59} and all age groups showed a decided preference for the 328 329 prosocial agent, no difference in empathic responding could be found. Chimpanzees produced 330 longer vocalizations indicative of emotional arousal during the punishment of the prosocial agent 331 that had directly interacted with them but no differential vocalizations occurred when they 332 witnessed the agent being punished following the indirectly experienced pro- and antisocial 333 behavior (regardless of her social orientation). Even though in chimpanzees it is difficult to 334 clearly label the valence of such vocalizations as they can reflect conflicting emotions⁴⁴, the 335 specificity of their occurrence (longer vocalizations during the hitting of the prosocial agent 336 compared to the antisocial agent) suggests that they might reflect something akin to empathic 337 distress. However, chimpanzees did not signal distress by attempting to escape witnessing the 338 punishment of the prosocial agent nor tried to approach and console the victim of the aggression as suggested by observational studies²⁰. These conflicting results (distress 339

vocalizations vs. non-escape/non-approach behavior) make it difficult to pinpoint the underlying
motivation of the chimpanzees' behaviors upon witnessing the punishment of the prosocial
agent.

343

344 There are some limitations to the present set of studies. One is the fact that interactions were 345 observed between individuals that were not of the same species as the subject. However, this 346 concern is reduced given that both chimpanzees and 6-year-olds responded differentially to the 347 two agents. While such cross-species set-ups are common in the study of social behavior of both human and non-human primates⁶⁰⁻⁶² future work will have to assess how far these findings 348 349 extend onto interactions with one's own species. Further, the different dependent variables for 350 the chimpanzees and the children (i.e. physical energy vs. valuable MUs) makes direct inter-351 specific comparisons difficult. While using different dependent variables has the advantage of 352 optimizing procedures for each species thus avoiding potential biases favoring one of the 353 species, future work may seek to expand the findings using the same dependent variables for 354 greater comparability of the effects. Finally, we were unable to counterbalance the 355 administration of the direct and indirect exposures to the pro- and antisocial in chimpanzees. 356 Our results, however, were consistent with the existing literature on the occurrence of 357 punishment following directly and indirectly experienced transgressions in chimpanzees, which 358 ameliorates to some extent the concerns derived from our current design.

359

360 We studied the evolutionary and ontogenetic origins of an increased motivation to watch the 361 punishment of antisocial others and their associated emotional states. Chimpanzees and 6-362 year-old children showed greater motivation by incurring costs to continue watching the 363 punishment of an antisocial over a prosocial agent. Furthermore, children displayed differential 364 responses of mixed positive and negative emotions when they witnessed punishment of 365 antisocial agents, which suggest that they might take some form of pleasure from this. Although 366 such a mechanism is still uncertain in chimpanzees, vocalizations of emotional arousal 367 produced when they witnessed the suffering of a prosocial agent, and their absence when 368 witnessing the suffering of an antisocial agent, might indicate that affective responses such as 369 pleasure may constitute an important motivational contributor to the exaction of revenge, with 370 early evolutionary origins. Crucially, chimpanzees did not vocalize differentially for the two 371 agents when seeing the two agents punished following indirectly experienced pro- and 372 antisocial behavior. Additionally, they did not engage in differential costs to witness the 373 punishment of the antisocial agent as compared to the prosocial agent. These findings provide

374 some evidence for the evolutionary origins of an increased motivation to watch punishment of 375 antisocial behavior with - at least in children- possible links to feelings of pleasure underlying 376 such a motivation. Such a motivation appears to develop at a protracted rate, similar to higher-377 level cognitive skills⁶³ and might emerge at an age at which children begin to care so much for 378 justice that they are willing to pay for it.

379

380 Methods and Materials

381 *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 written consent form to use the acquired data. Additionally, the chimpanzee work was approved by the MPI-EVA – Zoo Leipzig ethical committee.

387

388 Participants

389 Studies 1 and 3: In Study 1 we tested 17 chimpanzees (Pan troglodytes). There were 5 males 390 ranging in age between 8 and 38 years (M = 16 years and 8 months) and 12 females ranging in 391 age between 8 and 37 years (M = 22 years and 5 months). In Study 3, we tested 14 392 chimpanzees. There were 5 males ranging in age between 8 and 38 years (M = 15 years and 393 10 months) and 9 females ranging in age between 12 and 42 years (M = 27 years and 3 394 months). All chimpanzees were housed at the Wolfgang Koehler Primate Research Center, 395 Leipzig Zoo, Germany. Eleven of them participated in both studies, whereas the rest could not 396 do so because they were unavailable (see Table S1 for rearing history and detailed participation 397 in each study). All indoor and outdoor enclosures were furnished with vegetation, climbing 398 structures and visual barriers. Subjects were neither food- or water-deprived during the 399 experiment.

400

401 <u>Study 2:</u> We tested 72 children. There were three age groups: 24 4-year-olds (M = 4.15, age 402 range = 4.04-4.35), 24 5-year-olds (M = 5.04, age range = 4.97-5.4), and 24 6-year-olds (M =403 6.17, age range= 5.98-6.33). In each group there were equal number of boys and girls. Seven 404 children had to be removed from the analyses due to procedural error or fussiness. All 405 remaining subjects received all conditions. All children were recruited from a subject database 406 at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany.

408 Experimental Procedures

409 Studies 1 and 3: These two studies consisted of four phases: Training, Exposure, Preference 410 and Punishment (actual test). Before entering the Punishment phase, chimpanzees received a 411 sequence of training stages (see Training phase in SI) to ensure that they understood how to 412 open the heavy mesh sliding door that would allow them access to the adjacent room. After the 413 training, all subjects were exposed directly (Study 1) or indirectly (Study 3, by witnessing an 414 interaction between a human agent and a conspecific stooge) to two different human agents, 415 one at a time. The agents either acted prosocially towards the subject/stooge (Study1/Study3), 416 by providing food, or antisocially, by teasing and not allowing the subject/stooge to get access to 417 the food (see Exposure phase in SI). Whether the agent was prosocial or antisocial was 418 counterbalanced across subjects. To reduce carry-over effects between studies, different 419 agents participated in Study 3 (except for the punisher), which was conducted a few months 420 after Study 1. To test the efficacy of the Exposure phase a Preference phase was designed to 421 test for preferential begging from the two agents (see SI for more details). In the Punishment 422 phase (see SI for more details) either the prosocial or the antisocial agents entered the testing 423 room and sat in front of the Plexiglas window in the subjects' room. After 5 seconds of being 424 seated in front of the Plexiglas window (henceforth referred to as baseline period), a second 425 agent, the punisher, entered the room. The punisher approached the agent from behind with a 426 human facial expression of rage (henceforth referred to as pre-hit period) and started beating 427 her up (henceforth referred to as hit period) with a stick for 4 sec. (i.e., 4 hits with the stick, rate: 428 1 Hz). While being beaten up the agent cried out in pain. After the initial punishment period (i.e., 429 4 seconds) the agent either: 1) remained in her initial position for the whole time of the 430 punishment visible to the subject (10 more seconds, Figure 1A), so-called visible condition, or 2) 431 left her initial position (area A, see Figure 1A) and went into another area of the room invisible to 432 the chimp (area B, see Figure 1A) where the punishment continued for 10 more seconds, so-433 called *invisible* condition. If subjects wanted to continue watching the punishment in the invisible 434 condition they had to open the heavy sliding door (learned during the Training phase) and move 435 in front of the Plexiglas window in the new room. Similarly, if they wanted to escape from the 436 punishment in the visible condition happening in front of them, they had to operate the door to 437 move to another part of the room where this would then be invisible.

438

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 hoos considered as distress vocalizations⁴³ 442 and (waa) barks and (pant) hoots considered as display vocalizations⁴³. As previously 443 mentioned, vocalizations were categorized according to their acoustic structure and temporal 444 measures and grouped according to the call categories suggested by Goodall⁴⁴. Distress and 445 display vocalizations were lumped together and the combined results used for statistical 446 analysis. The duration of the calls was analyzed with the sound analysis software Avisoft and 447 Praat.

448

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 frequency of begs corrected for the amount of time spent in front of the correspondent human agent (Study 1: r =0.999, P = 0.028; Study 3: r = 0.997, p = 0.048),

456

457 <u>Study 2:</u> Children came into the lab accompanied by at least one parent. Parents had been 458 instructed before on the phone to bring six of their child's favorite toys, without the child noticing. 459 These were then taken by the experimenter and used as in the two exposure phases. Children 460 were given an initial endowment of 4 MUs. It was made clear that at the end of the experiment 461 each of the MUs could be traded for one sticker. The experimental procedure was demonstrated 462 using a miniature-sized puppet theatre.

463

464 Before the *Punishment phase*, each child was exposed consecutively to two different puppets, a 465 prosocial and an antisocial puppet (see Exposure phase in SI). Exposure entailed one of two 466 puppets to either act prosocially by returning three of the child's favorite toys, or antisocially, by 467 keeping them for itself. The puppets would bring up a toy from behind the theatre and hold it up 468 to the child. After telling the child that it wanted to play with them, the prosocial puppet would 469 hold the toy towards the child and put it into the child's hands, whereas the antisocial puppet 470 would withdraw as soon as the child reached for the toy. Similar procedures has been shown to elicit clear preferences in infants⁶⁴. Which puppet was prosocial or antisocial was 471 472 counterbalanced across subjects. Exposure and testing was performed for both puppets and 473 fully counter-balanced across all subjects. During the *Punishment phase*, the puppet to which 474 children had just been exposed remained on stage. After 5 seconds, another puppet appeared 475 (different to the two agents) carrying a long stick (punisher). The punisher started beating the

476 other puppet (prosocial/antisocial) up with the stick for 5 seconds (i.e., 5 hits with the stick, rate: 477 1 Hz). After the initial punishment period (i.e., 5 seconds) the theatre curtain closed rendering 478 both the punisher and the punished puppet invisible. The punisher puppet then returned and 479 said to the child that they were going to continue hitting the other puppet and that if the child 480 would like to continue watching then it should put one MU into a box to the right of the stage, 481 whereas if it did not want to continue watching it should put a MU into a box to the left of the 482 stage. Depending on where children placed their MU, the curtains were drawn again or not and 483 children could continue observing the punishment or not. In case they chose not to witness the 484 punishment, the punishment was still executed behind closed curtains. If children decided not to 485 continue watching on the first round then the punisher puppet did not ask again whether the 486 child cared for another round of witnessing punishment. However, if children decided to 487 continue watching, the punisher asked again after 5 seconds of punishment if they would like to continue watching. Given that children had received 4 MUs, the maximum number of paid 488 489 punishments was 4. Thus, all subjects received exposure to the first round of punishment and 490 the first question of whether they would like to continue watching or not. Depending on whether 491 children paid for punishment, they were asked again until they either decided to stop watching 492 or until they had no more MUs. The final round was the pursuit and punishment behind the 493 curtain, thus the child continued hearing the puppet crying for 10 more sec. but without visual 494 access to the punishment.

495

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

501

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).

506

507 At the end of the entire Punishment phase the experimenter showed the two agents to the child 508 and asked which puppet the child would rather play with, give a sticker to and thought was 509 nicer. From this a composite score of preference was obtained (see SI). 510

511 All data were analyzed in SPSS 23 (SPSS Statistics Software, IBM). No attempts to replicate

512 the findings reported in this paper have been made.

513

514 Data availability statement

- 515 The data that support the findings of this study are available from the corresponding author on
- 516 reasonable request.
- 517

518 Author Contributions

- 519 Conceived and designed the experiments: NM, NS, JC, TS. Performed the experiments: NB,
- 520 NM, NS. Analyzed the data: NM, NS. Interpretation of data and writing of the paper: NB, NM,
- 521 NS, TS, JC. Funding provided by JC and TS.
- 522
- 523

524 References

- 525
- 526 1 Nowak, M. A. Five rules for the evolution of cooperation. *science* **314**, 1560-1563 (2006).
- 527 2 Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity. (2005).
- 5283Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. The evolution of altruistic punishment.529Proceedings of the National Academy of Sciences 100, 3531-3535 (2003).
- 530 4 Fehr, E. & Gächter, S. Altruistic punishment in humans. *Nature* **415**, 137-140 (2002).
- 531 5 Henrich, N. & Henrich, J. P. *Why humans cooperate: A cultural and evolutionary* 532 *explanation.* (Oxford University Press, 2007).
- Henrich, J. & Boyd, R. Why people punish defectors: Weak conformist transmission can
 stabilize costly enforcement of norms in cooperative dilemmas. *Journal of theoretical biology* 208, 79-89 (2001).
- 536 7 Clutton-Brock, T. H. & Parker, G. A. Punishment in animal societies. *Nature* **373**, 209 (1995).
- 5388Hauser, M. D. Costs of deception: cheaters are punished in rhesus monkeys (Macaca539mulatta). Proceedings of the National Academy of Sciences 89, 12137-12139 (1992).
- 540 9 De Quervain, D. J., Fischbacher, U., Treyer, V. & Schellhammer, M. The neural basis of 541 altruistic punishment. *Science* **305**, 1254 (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).
- 545 11 Singer, T. *et al.* Empathic neural responses are modulated by the perceived fairness of others. *Nature* **439**, 466-469 (2006).
- 547 12 Batson, C. D. *The Altruism Question: Toward a Social-Psychological Answer*. (Erlbaum, Hillsdale, NJ, 1991).
- 549 13 Singer, T. *et al.* Empathy for pain involves the affective but not sensory components of pain. *Science* **303**, 1157-1162 (2004).

- Batson, C. D., Duncan, B. D., Ackerman, P., Buckley, T. & Birch, K. Is empathic emotion
 a source of altruistic motivation? *Journal of personality and Social Psychology* 40, 290 (1981).
- 15 Cools, A. K., Van Hout, A. J. M. & Nelissen, M. H. Canine Reconciliation and Third 555 Party Initiated Postconflict Affiliation: Do Peacemaking Social Mechanisms in Dogs
 556 Rival Those of Higher Primates? *Ethology* **114**, 53-63 (2008).
- 557 16 Palagi, E. & Cordoni, G. Postconflict third-party affiliation in Canis lupus: do wolves 558 share similarities with the great apes? *Animal behaviour* **78**, 979-986 (2009).
- 559 17 Seed, A. M., Clayton, N. S. & Emery, N. J. Postconflict third-party affiliation in rooks, 560 Corvus frugilegus. *Current Biology* **17**, 152-158 (2007).
- 561 18 Byrne, R. *et al.* Do elephants show empathy? *Journal of Consciousness Studies* **15**, 204-225 (2008).
- 563 19 Clay, Z. & de Waal, F. B. Bonobos respond to distress in others: consolation across the age spectrum. *PLoS One* **8**, e55206 (2013).
- 56520Romero, T. & de Waal, F. Chimpanzee (Pan troglodytes) consolation: third-party identity566as a window on possible function. Journal of Comparative Psychology 124, 278 (2010).
- 567 21 Mallavarapu, S., Stoinski, T., Bloomsmith, M. & Maple, T. Postconflict behavior in captive western lowland gorillas (Gorilla gorilla gorilla). *American Journal of Primatology* 569 68, 789-801 (2006).
- Langford, D. J. *et al.* Social modulation of pain as evidence for empathy in mice. *Science* 312, 1967-1970 (2006).
- 572 23 Bartal, I. B.-A., Decety, J. & Mason, P. Empathy and pro-social behavior in rats. *Science* 334, 1427-1430 (2011).
- 574 24 Burkett, J. P. *et al.* Oxytocin-dependent consolation behavior in rodents. *Science* **351**, 375-378 (2016).
- 576 25 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. *Cognitive development* 26, 30-39 (2011).
- Hamlin, J. K., Wynn, K., Bloom, P. & Mahajan, N. How infants and toddlers react to
 antisocial others. *Proceedings of the national academy of sciences* **108**, 19931-19936
 (2011).
- 583 28 Schulz, K., Rudolph, A., Tscharaktschiew, N. & Rudolph, U. Daniel has fallen into a 584 muddy puddle–Schadenfreude or sympathy? *British Journal of Developmental* 585 *Psychology* **31**, 363-378 (2013).
- 586 29 Shamay-Tsoory, S. G., Ahronberg-Kirschenbaum, D. & Bauminger-Zviely, N. There is no 587 joy like malicious joy: Schadenfreude in young children. *PloS one* **9**, e100233 (2014).
- 58830Tisak, M. S. Preschool children's judgments of moral and personal events involving
physical harm and property damage. *Merrill-Palmer Quarterly (1982-)*, 375-390 (1993).
- Jordan, J. J., McAuliffe, K. & Warneken, F. Development of in-group favoritism in 590 31 591 children's third-party punishment of selfishness. Proceedings of the National Academy of 592 Sciences of the United States of America 111. 12710-12715, 593 doi:10.1073/pnas.1402280111 (2014).
- 594 32 De Waal, F. B. Good natured. (Harvard University Press, 1996).
- 595 33 De Waal, F. B. & Luttrell, L. M. Mechanisms of social reciprocity in three primate 596 species: symmetrical relationship characteristics or cognition? *Ethology and* 597 *Sociobiology* **9**, 101-118 (1988).
- 598 34 Jensen, K., Call, J. & Tomasello, M. Chimpanzees are rational maximizers in an 599 ultimatum game. *science* **318**, 107-109 (2007).

- 600 35 Suchak, M. *et al.* How chimpanzees cooperate in a competitive world. *Proceedings of* 601 *the National Academy of Sciences*, 201611826 (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). *Journal of Comparative Psychology* **127**, 63 (2013).
- Russell, Y. I., Call, J. & Dunbar, R. I. Image scoring in great apes. *Behavioural Processes* 78, 108-111 (2008).
- 60838Jensen, K., Call, J. & Tomasello, M. Chimpanzees are vengeful but not spiteful.609Proceedings of the National Academy of Sciences 104, 13046-13050 (2007).
- 610 39 Matsusaka, T. When does play panting occur during social play in wild chimpanzees? 611 *Primates* **45**, 221-229 (2004).
- 612 40 Fabes, R. A., Eisenberg, N. & Eisenbud, L. Behavioral and physiological correlates of 613 children's reactions to others in distress. *Developmental Psychology* **29**, 655 (1993).
- 614 41 Eisenberg, N. *et al.* The relations of children's dispositional empathy-related responding
 615 to their emotionality, regulation, and social functioning. *Developmental psychology* 32,
 616 195 (1996).
- Valiente, C. *et al.* Prediction of children's empathy-related responding from their effortful control and parents' expressivity. *Developmental psychology* **40**, 911 (2004).
- A3 Nishida, T., Zamma, K., Matsusaka, T., Inaba, A. & McGrew, W. C. *Chimpanzee*behavior in the wild: an audio-visual encyclopedia. (Springer Science & Business
 Media, 2010).
- 622 44 Goodall, J. *The chimpanzees of Gombe: Patterns of behavior*. (MA: Belknap Press of 623 Harvard University Press, Cambridge, 1986).
- Riedl, K., Jensen, K., Call, J. & Tomasello, M. No third-party punishment in chimpanzees. *Proceedings of the National Academy of Sciences* **109**, 14824-14829
 (2012).
- 46 Anderson, J. R., Takimoto, A., Kuroshima, H. & Fujita, K. Capuchin monkeys judge third-628 party reciprocity. *Cognition* **127**, 140-146 (2013).
- 629 47 Smith, R. H. *et al.* Envy and schadenfreude. *Personality and Social Psychology Bulletin*630 22, 158-168 (1996).
- 48 Jordan, J. J., McAuliffe, K. & Warneken, F. Development of in-group favoritism in
 632 children's third-party punishment of selfishness. *Proceedings of the National Academy of*633 *Sciences* 111, 12710-12715 (2014).
- 634 49 Steinbeis, N. & Singer, T. The effects of social comparison on social emotions and
 635 behavior during childhood: The ontogeny of envy and Schadenfreude predicts
 636 developmental changes in equity-related decisions. *Journal of Experimental Child*637 *Psychology* **115**, 198-209 (2013).
- 638 50 McAuliffe, K., Jordan, J. J. & Warneken, F. Costly third-party punishment in young 639 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. *Developmental Science* 16, 952-958 (2013).
- 52 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. *Journal of Economic Behavior & Organization* **115**, 18-29 (2015).
- 53 Smith, C. E., Blake, P. R. & Harris, P. L. I should but I won't: Why young children 647 endorse norms of fair sharing but do not follow them. *PloS one* **8**, e59510 (2013).
- 64854Dunfield, K., Kuhlmeier, V. A., O'Connell, L. & Kelley, E. Examining the diversity of649prosocial behavior: Helping, sharing, and comforting in infancy. Infancy 16, 227-247650(2011).

- 55 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).
- 654 56 Grossbard, C. L. & Mazur, J. E. A comparison of delays and ratio requirements in self-655 control choice. *Journal of the Experimental Analysis of Behavior* **45**, 305-315 (1986).
- 656 57 Beran, M. J. & Evans, T. A. Delay of gratification by chimpanzees (Pan troglodytes) in 657 working and waiting situations. *Behavioural processes* **80**, 177-181 (2009).
- Eisenberg, N. *et al.* The relations of emotionality and regulation to dispositional and
 situational empathy-related responding. *Journal of personality and social psychology* 66,
 776-797 (1994).
- 59 Vaish, A., Carpenter, M. & Tomasello, M. Young children selectively avoid helping
 people with harmful intentions. *Child development* 81, 1661-1669 (2010).
- 663 60 Custance, D. M., Whiten, A. & Bard, K. A. Can young chimpanzees (Pan troglodytes)
 664 imitate arbitrary actions? Hayes & Hayes (1952) revisited. *Behaviour* 132, 837-859
 665 (1995).
- 666 61 Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P. & Bard, K. A. Imitative learning
 667 of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan
 668 troglodytes). *Journal of comparative psychology* **110**, 3 (1996).
- 669 62 Call, J., Hare, B., Carpenter, M. & Tomasello, M. 'Unwilling'versus 'unable':
 670 chimpanzees' understanding of human intentional action. *Developmental science* 7, 488671 498 (2004).
- 63 Hanus, D., Mendes, N., Tennie, C. & Call, J. Comparing the performances of apes
 673 (Gorilla gorilla, Pan troglodytes, Pongo pygmaeus) and human children (Homo sapiens)
 674 in the floating peanut task. *PloS one* 6, e19555 (2011).
- 675 64 Dunfield, K. A. & Kuhlmeier, V. A. Intention-mediated selective helping in infancy. 676 *Psychological science* **21**, 523-527 (2010).
- 677
- 678 679
- 680

683

- 681 **Competing interest statement**
- 682 The authors declare no competing interests.

684 Acknowledgments

685 We are grateful to Mike Tomasello for early input into the study design and to Matthias Allritz, 686 Vera Ehrich, Kerstin Esau, Elisa Felsche, Johannes Grossmann, Susan Hunger, Saskia Lorenz, 687 Julia Steinhardt, Katrin Schumann, Katja Waldherr and Katharina Wenig for helping with the 688 training phase and data collection with the chimpanzees at the Wolfgang Köhler Primate 689 Research Centre; to Yseult Heija-Brichard and Katrin Schumann for analyzing the chimpanzee 690 vocalizations, Katrin Schumann for analyzing part of the chimpanzee behavioral data, Markus 691 Neuschulz and Anja Hutschenreiter for reliability with the chimpanzee data, and to Christine 692 Brenner, Katharina Mueller, Charlotte Hoecker, and Jessica Buergel for the data collection with 693 the children. Thank you to Thibaud Gruber, Catherine Crockford, and Ammie Kalan for helping 694 us identifying some of chimpanzee vocalizations as well as Ammie Kalan for help with the 695 software Avisoft and Praat. Special thanks go to Henrik Grunert and Raik Pieszek for their help 696 in constructing the experimental apparatus. Thanks also to the zookeepers at the Leipzig Zoo 697 for their help with the chimpanzees. Salaries of N.S., N.M., T.S., as well as testing of the 698 children were supported by a Max Planck budget granted to T.S. as director of the Department 699 of Social Neuroscience. NS was supported by the European Research Council (ERC grant 700 agreement n° 715282, project DEVBRAINTRAIN), as well as a Jacobs Research Fellowship. JC 701 was supported in part by the European Research Council (ERC grant agreement n° 609819, 702 project SOMICS). NBG was supported by an FPU scholarship from the Spanish Ministry of 703 Education (Ref. FPU12/00409). With the exception of the Max Planck Society, none of the 704 funders played a role in study design, data collection and analysis, decision to publish, or 705 preparation of the manuscript

- 706
- 707

708 Figure Legends

709

Figure 1. Experimental Design for (A) chimpanzees and (B) children. Subjects (S) watch the punishment of a previously either prosocial or antisocial agent (A) by a punisher (P). 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. 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 in order to continue watching the punishment.

- 717
- 718
- 719

720 Figure. 2 Behavioral data and emotional indicators for chimpanzees (Study 1; N = 17) and 721 children (Study 2; N = 65). (A) More chimpanzees opened the heavy sliding door to continue 722 watching the punishment in the invisible antisocial (i.e. when punished and human agent left to 723 move to an invisible part of the room) compared to the invisible prosocial condition. Note, that 724 not all the chimpanzees opened the door. (B) All children paid to continue watching some of the 725 punishment, but only 6-year olds paid more to watch the antisocial agent being punished 726 compared to the prosocial agent. (C) Chimpanzees expressed greater distress vocalizations 727 when watching the punishment of the prosocial human agent. (D) Only 6-year old children

displayed more frequent smiles coupled with frowns during the punishment of the antisocialcompared to the prosocial agent. The error bars show s.e.m.

730

731

- Figure. 3 Behavioral data and emotional indicators for chimpanzees in Study 3 (N = 14). (A)
- 733 There were no differences in the chimpanzees' (A) behavior or (B) vocalizations between any of
- the conditions. The error bars show s.e.m.









