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11 Abstract

12 Cooperation plays a key role in the development of advanced societies and can be stabilized 13 through shared genes (kinship) or reciprocation. In humans, cooperation among kin occurs 14 more readily than cooperation among non-kin. In many organisms, cooperation can shift with age (e.g. helpers at the nest), however little is known about developmental shifts between kin 15 16 and non-kin cooperation in humans. Using a cooperative game, we show that 3-to-10 year-17 old French schoolchildren cooperated less successfully with siblings than with non-kin 18 children, whether or not non-kin partners were friends. Furthermore, children with larger 19 social networks cooperated better and the perception of friendship among non-friends 20 improved after cooperating. These results contrast with the well-established preference for 21 kin-cooperation among adults and indicate that non-kin cooperation in humans might serve to 22 forge and extend non-kin social relationships during middle childhood and create 23 opportunities for future collaboration beyond kin. Our results suggest that the current view of cooperation in humans may only apply to adults and that future studies should focus on how 24 25 and why cooperation with different classes of partners might change during development in 26 humans across cultures as well as other long-lived organisms.

27

28 Keywords

29

Kin selection, Kinship, Evolution of cooperation, Children development, Human Evolution

30 Introduction

31 Cooperation is thought to have played a key role in the evolution of advanced 32 societies, especially in humans [1–7]. Both kin-based interactions and reciprocity can 33 promote cooperation while protecting against cheating [2–6]. Cooperation among kin can 34 mean that benefits to the recipient of help can lead to indirect genetic benefits to the donor, an 35 evolutionary process called "kin-selection" [8], as described in social insects [9,10] and a 36 number of vertebrates [11,12]. Alternatively (or additionally), unrelated individuals who 37 interact repeatedly can *reciprocate* leading to benefits to each individual in the partnership 38 across time [13,14] such as egg trading in fish [15,16] and allogrooming in primates [17]. 39 More recently, a few studies have shown that both mechanisms can operate in tandem with 40 one mechanism playing a more important role in cooperation for a given system. For 41 example, food sharing in vampire bats is clearly maintained by reciprocity even if such 42 sharing can occur among kin adding further indirect benefits [18–20]. Likewise, cooperation 43 in humans occurs both among kin [21,22] as well as through reciprocal interactions [6,23– 44 27], although human adults clearly favor cooperation with kin over strangers [28–31]. 45 In many organisms, the form of cooperation can change with age. For example, young 46 individuals act as helpers in cooperative breeding birds but adults do not [32,33] whereas the opposite is true in many cooperative breeding mammals [34]. Whether similar shifts occur 47 48 with age in systems where both kin and non-kin cooperation occur either in absolute terms or 49 in the relative importance of each form of cooperation, is unknown. Studying the 50 development of kin and non-kin cooperation is critical to our understanding of the evolution 51 and function of cooperation in longer-lived organisms and their role in the development and 52 evolution of advanced societies [7,35]. Surprisingly, appropriate experimental tests in humans are still lacking. Among the limited number of experimental studies comparing kin 53 54 and non-kin cooperation or prosociality in children, reciprocation seems to be important [36-

55 39] but children tend to favor sharing with their relatives compared to strangers [40,41] like 56 adults. However, previous experimental studies of kin-sharing in children use third party tasks, where participants are asked about abstract scenarios, and these tests often give 57 58 different results from direct participation in a task [42,43] since it reflects what the participant 59 thinks another person should do but not necessarily how they would actually behave in a real 60 cooperative situation (see however Crittenden et al. [31]). In addition, third party tasks are 61 thought to be "removed from the evolutionary mechanisms that [...] likely shape these 62 phenomena in early ontogeny" and do not "reflect the effects of the collaborative foraging 63 context of early humans, in which one shares the spoils [...] among those who took part in the *collaborative effort*" [43]. Because no experimental study in children has directly 64 65 compared kin and non-kin cooperation in situations in which individuals are asked to actively 66 collaborate in a realistic setting, little is known about the development of kin and non-kin 67 cooperation in humans with age.

Here, we used a direct-action cooperation task to evaluate if children cooperate more 68 69 with kin, friends, or non-friends when actively engaged in a game that requires children to 70 cooperate and coordinate actions with other children. We measured cooperation using a rope 71 pulling task (Fig. 1A) in which two children coordinate in pulling a single rope to reach a reward and succeed only if both rope ends are pulled at the same time and same speed [44– 72 73 46]. This task is complex and needs the active engagement of children in the task since it 74 requires paying attention to the partners' actions to succeed. While a previous experiment 75 using this design began by giving the children a demonstration, we decided to render the task 76 more difficult by omitting the demonstration and merely telling the children that they would 77 have to work together to complete the task [46]. To examine the roles of kinship and friendship on performance by children of a cooperative task, we assigned each child a partner 78 79 who could be classified as kin (a sibling), a socially close non-kin (a "best friend") or a

socially distant non-kin (a non-friend). Pairs were quasi-randomly assigned by the
experimenter based on questionnaires administered to teachers and children before the task
(see methods) and each pair was allowed to conduct the task until successful or up to three
attempts if unsuccessful. In so doing, we investigated whether joint success in a cooperative
task was linked to the degree of relatedness between partners in children. We found that
children cooperate more efficiently with non-kin (friends and non-friends) than with kin (i.e.
siblings) partners.

87 Methods

88 <u>Participants</u>

We recruited 290 children from ages 3 to 10 (92 3-to-5 year-olds, 139 6-7 year-olds 89 90 and 59 8-to-10 year-olds; 135 females) from 15 kindergartens and elementary schools in 91 southwestern France. While this age range is large, it reflects all children that potentially interact within schools where the study was conducted as many schools have mixed level 92 93 classes and a common play area. All parents signed an informed consent form for their 94 children and only children who gave their verbal assent were included. Parents also filled a 95 demographic questionnaire including parents' income, living area (urban vs. rural), number 96 of siblings and native language. Thirty percent of children were from middle-class backgrounds (20,000 to 30,000 euros/year) and 35 % lived in urban areas. Participants had 97 98 2.5 siblings on average: 18% were an only child, 44% had only one sibling, 20% had two siblings and 18% had more than 2 siblings. Sixty-nine percent of the children were native 99 100 French and all children (except 2 children from whom the test was performed in English) 101 were French-speaking. The same female experimenter tested children during a single videorecorded session in an available room at their schools. 102

103 *Experimental procedure*

104 Participants performed a rope pulling task [44] that requires coordinated pulling to 105 reach a reward (see Fig. 1 and Fig. S1). Two children are required to pull their end of the rope 106 simultaneously, each holding the end of the same rope where the two ends are far enough 107 apart that one person could not reach both ends at the same time. A single rope is threaded 108 around an apparatus such that only if both rope ends are pulled at the same time can the 109 containers be moved and the rewards be reached. Pulling on one end would only move the 110 rope but not the two sliding containers which contain the rewards, making the other end of 111 the rope unavailable to a partner. Only if both participants pulled the rope at the same time 112 and at similar speeds, would they each obtain a reward (i.e. joint success, with no delayed 113 reciprocity). Two cases lead to failure in the cooperative task: asymmetric pulling led to 114 neither participant obtaining the reward (0/0) or if both participants pulled at the same time 115 but one let go after gathering their reward but before their partner could take their own 116 reward such that just one of the two obtained the reward (0/1 or 1/0). If only one child took 117 his/her own sticker, the sticker was put back into the sliding container and children began a 118 new trial together.

The Experimenter (E) explained to the children that they would play together to each win a reward (stickers) but provided no further instruction. By not providing more guidance, this cooperative task was rendered more difficult than in previous studies using the same game (63% success here vs. 94% success during first trials in a previous study [46]). E placed the two rewards (one for each child) in the apparatus (one in each container of the apparatus) under observation of the children and told them they could start to play.

Each time a pair attempted to pull the ropes is termed a "trial". Our measure of cooperation and coordination was focused on a single trial, but upon request of teachers to not create inequalities in the classroom, dyads of children could perform a maximum of 3 trials beyond which E stopped the testing and gave the stickers to the children. As such, we 129 focused our analyses on the first trials to avoid any impact of learning on joint success in 130 subsequent trials. Overall, most children succeeded within those 3 trials as 63% (91/145) of 131 the pairs succeeded in the first trial, 21% (31/145) in the second trial, 6% (9/145) during the 132 third trial, and only 10 % (14/145) of dyads did not succeed by the 3 trial. In supplemental 133 information, we provide additional analyses of these subsequent trials which reinforces 134 results from the first trial only (see supplemental results, Table S1 and Fig. S2). Overall the 135 sample included 39 pairs of siblings, 52 pairs of friends, and 54 pairs of non-friends who 136 performed 77, 71 and 67 trials respectively, corresponding to a total of 215 trials among 145 137 dyads.

138 The partners of a dyad could be either siblings, friends (someone they frequently play 139 and interact with), or non-friends (someone they know but do not particularly interact with). 140 The status of the dyad (i.e., siblings, friends, non-friends) was determined before conducting 141 the experiment by asking the children's teachers to name the friends of the participants and 142 specifying each participant's best friend through a questionnaire filled out before the 143 experiment. We asked teachers to base their estimation of relationship closeness of a dyad on 144 the amount of time children spent together, intensity of positive interactions, and time they 145 play with each other at school [47,48]. Based on the responses of the questionnaires, dyads 146 were formed by E. Following the definition of friendship in the literature [49], "friends" were 147 formed by dyads where both children considered the other their best friend and "non-friends" 148 were formed among two individuals where neither considered the other a friend. 149 Furthermore, "non-friend" dyads specifically avoided matching individuals who have 150 conflictual relationships. Finally, kin status was assigned to any siblings within the class or 151 between two classes in the school. Because it was more rare to find siblings given logistical 152 constraints at schools, possible sibling dyads were formed as a priority. Remaining 153 individuals were then assigned to the other two categories at random. Given that kin dyads

naturally showed larger age and sex differences than friend dyads (often same age and same
sex), the "non-friend" dyads were balanced by matching both pairs of the same age and same
sex children and pairs with large age differences and different sex to be more similar to the
kin category (see Fig. S3).

158 In order to confirm the assignation of the dyads based on teacher evaluation of friendship, a 159 questionnaire for children was also performed. E asked children about their relationship with 160 their partner ("Do you like to play with CHILD X?") and about the quality of their 161 relationship using an emoticon Likert scale ("How much do you like to play with CHILD X?: 162 a lot, a little, not at all) [50]. The order of the emoticons was counterbalanced across 163 participants to avoid bias. In order to investigate whether participation in the rope pulling task 164 affected the relationship of the partners, the same questions were administered 24 h after the 165 test. Finally, we gathered information about each child's friend network before the experiment, by asking the child to name their friends ("Please, tell me the names of the 166 children you like to play with the most?"). Due to logistical constraints, we were only able to 167 168 gather complete friendship network data at 10 of the 15 schools in our sample.

169 *Data coding*

170 All trials were recorded using a video camera oriented so that both participants and 171 the apparatus were visible allowing us to score the children's performances. Successful trials 172 were scored when both partners pulled together and successfully reached the reward (i.e. joint success). Failed trials were scored when children failed to pull the rope together such that 173 174 neither reached the reward or when only one child reached the reward. The same trained 175 research assistant coded the number of gazes (each movement of the eyes accompanied by a movement of the head toward the partner) of each dyad blind to dyad category for the first 176 trial only of each dyad. The number of gazes included situations when both partners look at 177 178 each other and when a single individual looks at the other one.

179 <u>Statistical analysis</u>

180 All analyses were performed in the R environment for statistical computing version
181 3.3.6 (R Development Core Team, 2018).

182 We examined the effect of partner relationship within a dyad on joint success using a 183 binomial GLM [51] including the first trial (0 vs. 1) performed by each dyad. We built a full 184 model that included fixed effects of dyad relationship (kin, friend, non-friend), dyad sex 185 (male-male (MM), female-female (FF), male-female (MF)), average age of partners and age 186 difference between the partners. Since nearly all dyads eventually succeeded in performing 187 the task by the third trial (see above), analyses of the change in relationship between a pair 188 could not be compared between pairs that succeeded in the first trial relative to those who did 189 not and so simply included all individuals.

190 Coordinated rope pulling could be facilitated by looking at a partner, so we looked at 191 the impact of gaze frequency (gazes per second) on joint success in the first trial (0 vs. 1) 192 performed by each dyad using a GLM. We built a full model that included fixed effects of 193 dyad relationship (kin, friend, non-friend), dyad sex (MM, FF, MF), average age of partners 194 and age difference between the partners. We also investigated the effect of partner status on 195 the number of gazes using a LM including gaze frequency (gaze per second) during the first 196 trial. We included dyad relationship (kin, friend, non-friend), dyad sex (MM, FF, MF), 197 average age of partners and age difference between the partners as fixed effects.

We then assessed the relationship between performance in the task and the size of a child's social network. Using a binomial GLM, we asked whether performance (0 vs. 1) during the first trial was affected by a child's number of friends (i.e. outdegree centrality in social network analysis) while controlling for dyad sex, mean age of the dyad, age difference of the dyad partners, and number of children in the classroom.

For GLMs, visual inspection of residual plots using the DHARMa package [52] did not reveal deviations from homoscedasticity or normality. For each fixed effect, statistical significance was evaluated by likelihood ratio tests of the full model against the same model without the tested fixed effect. In supplemental tables, we report odd-ratios and their corresponding 95% confidence intervals, p-values as well as marginal, conditional or pseudo R2 of the Full Model when appropriate.

Finally, we tested the effect of the rope pulling task on the quality of the relationship between the two partners, we performed McNemar and Cochran Q test when appropriate on kin, friend and non-friend partners separately.

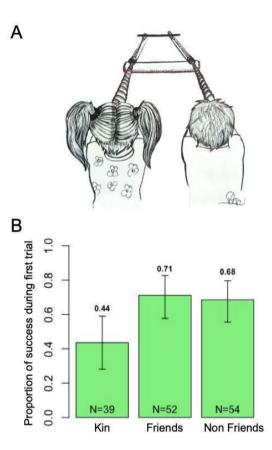
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213 Results and discussion

214 During first trials, 63% (91 out of 145 trials) of the children jointly succeeded in the 215 cooperative rope pulling task. We found that children cooperate less well with kin than with 216 non-kin (Fig. 1B): the likelihood of cooperating during the first trial was significantly 217 affected by dyad type while controlling for mean age, age difference and sex of dyads 218 (binomial GLM, partner status: P=0.019, mean age: P=0.008; age difference: P=0.084, sex: 219 P=0.81; Fig. 1B and Table S2). Friends (52 dyads, 71% successful; z=2.62; P=0.009) and 220 non-friends (54 dyads, 68 % successful, z=2.29; P=0.022) were more likely to succeed on 221 their first cooperative trial than kin partners (39 dyads, 44%, Fig. 1B and Table S2) whereas 222 performance of friends and non-friends did not differ from each other (z=-0.61; P=0.54; Fig. 223 1B and Table S2). There was no effect of an interaction between the mean age of the dyad 224 and partner status (mean age \times partner status: deviance= -0.056; P=0.97) nor between age 225 difference of the dyad and partner status (age difference × partner status: deviance: 1.22 226 P=0.54) suggesting that any shifts in cooperative preferences towards kin with age must

227 occur beyond 8-10 years-old (Fig. S4). These patterns were consistent when controlling for

demographic information (Table S3) and restriction to subsets of the data (Figs. S4, S5).



229

230 Fig. 1. Performance in the cooperative rope pulling task by partner status. A) Illustration of the cooperation apparatus. The "rope pulling game" was adapted from previous studies on 231 chimpanzees and children [46,54]. Photograph of the apparatus is also provided in Fig. S1 232 233 in supplemental information (SI). B) Proportion of successful first trials of kin (i.e. siblings) and non-kin friend and non-friend dyads in cooperative rope pulling. Error bars indicate 234 235 95% bootstrapped confidence interval. N values indicate the number of dyads in each 236 category (i.e. kin, friends, non-friends). Kin partners were less successful than non-kin in the 237 rope-pulling task.

239	The contrast in the	propensity to	cooperate with k	in relative to	non-kin between
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- studies in adults [21,22,53] and our results in children suggest that there is a striking
- 241 developmental shift in the value of different forms of interactions. We could not run the same
- exact study in adults since the task would be far too easy for them and so could not directly
- 243 contrast preferences in adults and children using the same population. However, studies in

adults show a very consistent pattern of kin preferences over non-kin across a broad variety 244 of experimental paradigms (e.g. public good game, prisoners' dilemma) and populations. For 245 246 instance, adults from Western industrialized countries trust kin more [21], are more likely to 247 cooperate with individuals who have similar facial features to their own [22], and minimize 248 punishment after rule transgression for kin compared to strangers [55,56]. Furthermore, non-249 Western traditional societies show comparable preferences for cooperation with kin [57,58]. 250 While we did find an improvement in joint success in the cooperative task with age (Fig. S4 251 and Tables S2 and S3), this improvement did not alter patterns of cooperation between kin 252 versus non-kin (i.e. no significant interaction effect reported above; Fig. S4) while controlling 253 for dyad age suggesting that contrasts between children and adults in their preference for 254 cooperating with kin are not simply due to an improvement of solving a cooperative task. 255 Well known cooperative systems shift from cooperation among kin to no cooperation or the 256 reverse with age [32] [33] [34], but to our knowledge, such age related shifts in cooperative 257 preferences have not yet been examined experimentally in systems where both kin and non-258 kin cooperation coexist. For example, it would be interesting to know if vampire bats which 259 show reciprocal cooperation with non-kin more so than kin among adults show a strong 260 preference for food sharing among kin rather than non-kin among juveniles. Knowing if such shifts are general will require both a concerted effort to document more cases of kin and non-261 262 kin cooperation in the same system as well as tests of cooperative preferences with age. 263 Shifts in preferences for cooperating with kin vs. non-kin may be a consequence of a 264 shift in the value of cooperating with different classes of individuals with age. Kin 265 cooperation among adults might provide the greatest direct and indirect benefits to success 266 (e.g., fitness, wealth, etc. [60]) since they have reached reproductive maturity where gene

transmission is likely more important than reciprocity thereby favoring kin interactions andindirect genetic benefits from cooperation. On the other hand, children are far from

reproductive age and therefore might invest primarily in resource acquisition and survival which can benefit from reciprocal cooperation with peers regardless of kinship. Furthermore, kin-competition might reduce the value of kin-cooperation among children (e.g. siblings) [61–63] especially if resources are primarily provided by parents [43]. The benefits of a given cooperative interaction to success in children are indeed modest given that children are still supported by their parents and instead may serve primarily to develop cooperative skills needed for the future such as building a social network [64].

Developing friendships and affiliations with peers in mid-childhood has indeed been linked to future success at adulthood [60,65,66]. Since the current network of young children is still fairly limited, reinforcing and increasing reputation through reciprocity and building a broader social network might thus be more important during childhood than adulthood.

280 Indeed, social networks tend to expand in size among young adults, but shrink in older adults

[67]. Here, we found that having a bigger social network before the experiment was related to

subsequent performance during the first trial in the rope pulling task (Fig. 2) after controlling

for the age difference between partners, mean age, sex and number of children in the

284 classroom (binomial GLM, out degree centrality or number of friends named by participants:

deviance=5.61; P=0.018, mean age: deviance=10.27; P=0.001; age difference:

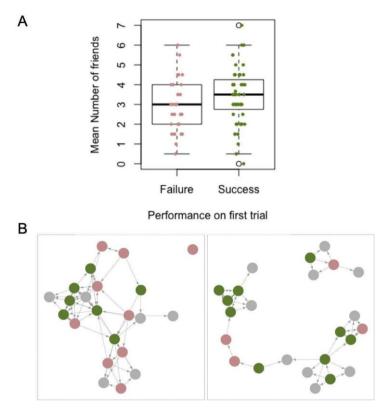
deviance=3.14; P=0.076, sex: deviance=2.12; P=0.35; number of children in the classroom:

deviance=1.12; P=0.29; Fig. 3, Fig. 2, Table S4 and Fig. S6). This correlative relationship

could exist either because social individuals cooperate more readily or because those who

289 have built a bigger network develop cooperative skills. Regardless of directionality, our

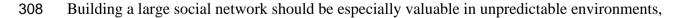
290 results show a cooperative benefit to a larger social network.



292

293 *Fig. 2. Relationship between the number of friends (out degree centrality) and performance* 294 in the rope pulling task. The number of friends and social network were based on a 295 questionnaire before the experiment where children were asked to give the names of children they prefer to play with in their classroom including children who did not participate in the 296 297 task. A) Boxplots contrasting the number of friends averaged between the two partners 298 according to their performance during the first trial. Failure in the first trial is shown in red 299 and joint success in green. Each dot represents a dyad of children. B) Examples of two 300 classroom networks in which individuals who succeeded in the first trial appear in green and 301 who failed in red. Children who did not participate and who participants named as friends 302 appear in grey. Arrows represent friendship between children such that bi-directional arrows 303 represent pairs of individuals who each listed the other as a friend whereas single headed 304 arrows represent cases where one individual considered the other a friend while the second 305 individual did not list the first as a friend. All networks are presented in Fig. S6. Having more 306 friends is linked to a higher success in the cooperative task.

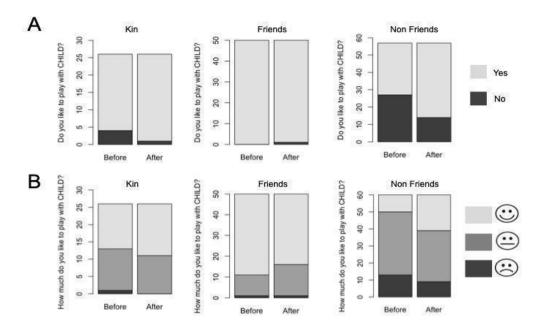
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309 since extending one's social network to cooperate with non-kin could provide benefits when

- the social community is perturbed whereas limiting one's social network only to kin would be
- risky [18,19]. For example, under unpredictable/risky situations [19,68] or when non-kin are
- more numerous than kin [18], different species of mammals (e.g. bats [19], primates and
- dolphins [68]), tend to favor cooperation with non-kin compared to kin partners. For children,

314 the school environment is constituted mostly of non-kin and has some risks (e.g. 315 victimization by peers [69–71]), so expansion of the social network could indeed carry 316 "social bet hedging" benefits. If cooperation serves to strengthen or build a social network, 317 we would predict that participation in a cooperative action should alter future interactions. As 318 such, we investigated whether performing the rope pulling task subsequently modified the 319 relationship between the two partners. To do so, children were asked to rate their relationship with their partner before and again one day after the cooperative task (Fig. 3) using a Yes/No 320 preference test ("Do you like to play with CHILD X?"; Fig. 3A) and an emoticon Likert scale 321 ("How much do you like to play with CHILD X? A lot, a little, not at all"; Fig. 3B). We 322 323 found that the relationship quality of non-friends improved after performing the rope pulling task together in both the Yes/No preference scale (McNemar $\chi^{2^{(1,56)}}$ =9.60; P = 0.002; Fig. 3A) 324 325 and the Emoticon Likert scale (Cochran Q(1,55)=7.35; P=0.007; Fig. 3B). As expected, we 326 did not detect a change in how much children liked kin partners (Yes/No preference test: McNemar χ^{2} ^(1,25)=1.33; P=0.25; emoticon Likert scale: Cochran Q^(1,25)=1.80; P= 0.18; Fig. 3) 327 and friend partners (Yes/No preference test: McNemar $\gamma 2^{(1,49)}=1$; P=1; emoticon Likert scale: 328 Cochran $Q^{(1,49)}=2.78$; P=0.10; Fig. 3) after the task since kin and friends already liked their 329 dvad partners in nearly all cases before performing the cooperative task (Fig. 3). 330



332 Fig. 3. Effect of the cooperative task on the relationship quality between kin, friend and non-333 friend partners. A) Results from the Yes/No preference scale in which children were asked to 334 answer the following question, before and after the rope pulling task: "Do you like to play with CHILD X?". "Yes" responses appear in light grey and "No" responses in dark grey. B) 335 336 Responses from the Emoticon Likert scale during which children were asked to rate how 337 much they like to play with their partner twice (before and after the rope pulling task). They can either respond "A lot" in light grey, "a little" in medium grey or "not at all" in dark 338 grev while pointing to a "smilev scale" corresponding to each level. Perceived relationship 339 340 quality of non-friends improved after cooperating.

341

342	Overall, our results show that cooperation between non-kin partners plays a key role during
343	childhood which we argue serves to expand a child's social network since non-friends had a
344	more positive view of their "unknown" partner after interacting during the cooperative task.
345	These results contrast with two studies in which children had to choose how to allocate
346	resources between dolls (i.e. third party tasks with fictional characters) which both showed
347	greater apparent cooperation with kin than friends or strangers [e.g. 40,72]. We believe that
348	differences in experimental methods lead to this contrast since the use of fictional characters
349	is more likely to elicit a response that reflects what children think they or others <i>should</i> do
350	[42,73] whereas direct interactions to cooperate in a face-to-face situation used in our
351	experiments should better reflect the actual outcome of natural cooperative situations.

352 Furthermore, direct tasks are more challenging than simple allocation tasks such that costs of 353 cooperation could also alter decisions. A difference in the value of friendships vs. sibling 354 relationships among children relative to adults might drive contrasts in how much effort each 355 group put into the cooperative task. The rope pulling task used here requires continued, active 356 attention and coordination with a partner to succeed. Indeed, we observed that most of the 357 unsuccessful trials happened either when a child pulled the rope before the other could grab 358 it, or when a child let go of the rope before his/her partner could grab their own reward. We 359 hypothesized that one possible explanation of failure could be a lack of attention between the 360 two partners. Consistent with this idea, the number of gazes during the first trials was indeed 361 a strong predictor of joint success (Fig. S7 and Tables S5) and kin dyads displayed fewer 362 gazes than other types of dyads (friends partners: P < 0.005; non-friends: P=0.056; Fig. S7). 363 Using this direct-action cooperation task, we found that children cooperate more with non-kin 364 peers compared to siblings in direct contrast with results in adults. Given the difficulty of our 365 cooperative task for children and considering the time children in western societies spend at 366 school, we believe our results reflect an ecologically realistic measure [74] of cooperation in 367 schoolchildren, at least in France. However, the value of cooperation with kin versus non-kin 368 could vary by context or culture and it would be interesting to see if our results hold in other 369 populations. Indeed, a more complete understanding of how decisions about cooperation shift 370 through life will require both attention to the context of testing (e.g. [75]) and application of 371 similar direct-interaction tests in individuals from a broad age range and across cultures. 372 Whether such developmental shifts in cooperation are common in other organisms also 373 remains to be explored, but should exist in cases where the benefits of cooperating with 374 different types of partners shifts through life [76]. This new hypothesis motivated by our 375 findings challenges our understanding of cooperation and should stimulate new research into 376 cooperation across life stages in both humans and other social organisms.

377 References

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576 G. B. -J., A. S. C, M.B and A.H. designed research; G. B. -J and A. R. performed research;

577 M. C. and G. B. -J. analyzed data; G.B.-J, A.S.C and M.C. wrote the paper; M. B. and A.H.
578 gave feedback on the paper.

579 Additional Information

580 Supplementary Information is available for this paper. Correspondence and requests for

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