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Title: Bonobos prefer individuals that hinder others
over those that help

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24 **Summary:** Humans closely monitor others' cooperative relationships [1, 2]. Children and adults
25 willingly incur costs to reward helpers and punish non-helpers—even as bystanders [3-5].
26 Strikingly, by three months, infants already favor individuals they observe helping others [6-8].
27 This early-emerging prosocial preference may be a derived motivation that accounts for many
28 human forms of cooperation that occur beyond dyadic interactions and are not exhibited by other
29 animals [9, 10]. As the most socially-tolerant nonhuman ape [11-17, but see 18], bonobos (*Pan*
30 *paniscus*) provide a powerful phylogenetic test of whether this trait is derived in humans.
31 Bonobos are more tolerant than chimpanzees, can flexibly obtain food through cooperation, and
32 voluntarily share food in captivity and the wild, even with strangers [11-17, but see 18]. Their
33 neural architecture exhibits a suite of characteristics associated with greater sensitivity to others
34 [19, 20], and their sociality is hypothesized to have evolved due to selection against male
35 aggression [21-23]. Here we show in four experiments that bonobos discriminated agents based
36 on third-party interactions. However, they did not exhibit the human preference for helpers.
37 Instead, they reliably favored a hinderer that obstructed another agent's goal (Experiments 1-3).
38 In a final study (Experiment 4), bonobos also chose a dominant individual over a subordinate.
39 Preferring hinderers may reflect attraction to dominant individuals [24]. A preference for helpers
40 over hinderers may therefore be derived in humans, supporting the hypothesis that prosocial
41 preferences played a central role in the evolution of human development and cooperation.
42
43 **Keywords:** prosocial preference, prosocial motivation, social evaluation, third-party knowledge,
44 cooperation, human evolution, human development, bonobo, great ape

45 **RESULTS**

46 The prosocial preference hypothesis suggests that bonobos exhibit their distinct pattern of
47 cooperation in part because they share a preference with humans for those who are prosocial
48 toward others. Alternatively, the dominance hypothesis suggest that, while the outcome of
49 bonobo cooperation is often human-like, bonobos, unlike humans, are more attracted to
50 individuals who are antisocial in third-party interactions as these individuals are more likely to
51 be dominant, powerful allies [25-28]. To test the prosocial preference and dominance
52 hypotheses, we showed bonobos displays in which one actor behaved prosocially and another
53 antisocially toward a third-party in one context. Then we allowed bonobos to choose between the
54 actors in a completely unrelated context.

55 **Experiment 1: Bonobos prefer animated agents that hinder others**

56 Twenty-four bonobos participated in Experiment 1 (12 females, $M_{age}=10.42$ years,
57 range=4-19 years; Table S1), completing both a test and control condition on separate days with
58 condition order counterbalanced across subjects. In each condition, the experimenter sat at a
59 table just outside the subject's enclosure, attracted them with food, and showed the subject two
60 different animated videos on an iPad. The videos, modeled closely after the stimuli used by
61 Hamlin, et al. [6] to test human infants, depicted a pair of 2-dimensional shapes interacting. As
62 cues to their agency, each shape had two eyes with white sclera and dark pupils, and exhibited
63 goal-directed movements [29]. Eyes were chosen since experiments have shown that apes are
64 sensitive to eye contact and direction [30], and bonobos are even more sensitive to eye gaze than
65 chimpanzees [31]. In the test condition, each video began with a circle, the Climber, entering the
66 scene and attempting but failing three times to climb a steep hill. On the third attempt, the
67 climber encountered another agent. In the *helper animation* (Figure 1A; Movie S1), a second

68 shape (i.e., the helper; e.g., a blue triangle) entered from below and pushed the climber up to the
69 top of the hill before returning down the hill and exiting the screen. In the *hinderer animation*
70 (Figure 1B; Movie S1), a different shape (i.e., the hinderer; e.g., a red square) entered from
71 above and pushed the climber back down the hill before returning to the top of the hill and
72 exiting the screen. Videos were of equal length and the helper and hinderer each spent
73 approximately the same amount of time on screen and in contact with the climber.

74 Following Hamlin, et al. [6], two control animations were designed to examine the
75 influence of the nonsocial features of our experimental animations. Each control animation was a
76 variant of an experimental video in which an agent pushed an eye-less, inanimate circle up or
77 down the hill (see Figure 1C-D). Unlike the climber in the experimental animations, the
78 inanimate circle in these control videos exhibited no independent movement or goal-directed
79 action. Otherwise, the *upward animation* (Movie S1) mimicked the actions of the helper
80 animation and the *downward animation* (Movie S1) mimicked those of the hinderer animation.

81 Test and control sessions each involved four trials in which subjects first witnessed the
82 two animations for that condition in a loop (i.e., test: helper and hinderer animations, control:
83 upward and downward animations) and then were allowed to choose between paper cutouts of
84 the agents placed on top of small pieces of apple (Movie S2). Based on previous work with
85 infants and nonhuman apes, we used reaching behavior as a measure of preference [e.g., 6, 32].
86 To avoid shaping subjects' preferences non-differential rewarding was used. Subjects received
87 the same quality and quantity of food regardless of their choice. The helping and hindering
88 behavior in the test events did not involve food. Therefore, a preference, for example for helpers,
89 could not be based on subjects evaluating the agent as a social tool for food acquisition. Unless

90 otherwise noted, all analyses for all experiments represent two-tailed one-sample Wilcoxon
91 signed rank tests of the proportion of trials in which subjects chose a particular agent.

92 The bonobos exhibited a significant bias for selecting the hinderer [$N=24$,
93 $M=0.625\pm SE=0.043$, $p=0.011$; see Figure 2A]. Only two individuals chose the helper on a
94 majority of trials while 11 favored the hinderer. This finding suggests that bonobos can
95 discriminate between prosocial and antisocial agents but that they do not show the human
96 preference for prosocial agents. Separate analysis of adult (age 9 and above) and subadult
97 subjects revealed that only adults showed a significant preference (Figure 2A; see Supplemental
98 Information for details). Because the youngest testable bonobos were already 4-years-old, we
99 cannot be certain about the preferences of younger infants. However, we found no evidence that
100 bonobos discriminate helpers from hinderers, or at least that they exhibit strong social
101 preferences based on third-party interactions, until adulthood—in contrast to humans' early
102 emerging prosocial preference.

103 If bonobos were responding to perceptual rather than social features of the animations,
104 they should prefer the downward agent whose movements mirrored those of the hinderer.
105 However, subjects showed no preference for either agent in the control condition when grouped
106 together [$N=24$, $M=0.438\pm 0.035$ choice of downward agent, $p=0.084$; see Figure 2A] or
107 separated into adults and subadults (see Supplemental Information). A direct comparison of the
108 experimental and control conditions also revealed a significant difference in choice patterns
109 [related samples Wilcoxon signed rank test, $z=-2.884$, $N=24$, $T+=13$, $\text{ties}=9$, $p=0.004$], with
110 subjects selecting the hinderer significantly more than the downward control. Thus, perceptual
111 features alone do not appear to explain bonobos' preference for the hinderer.

112 **Experiments 2 and 3: Bonobos prefer unfamiliar human actors that hinder others**

113 The preferences we observed for arbitrary shapes acting with agency may translate into
114 the natural social interactions of bonobos. However, in a previous experiment, bonobos did not
115 discriminate between human experimenters they observed either attempting to share food with or
116 steal food from another experimenter [33]. Therefore in Experiment 2, we tested whether the
117 hinderer preference from Experiment 1 is robust enough to generalize to a real world social
118 interaction involving object-centered prosocial and antisocial behavior by unfamiliar human
119 actors.

120 Twenty-two bonobos (ages 4-17, 11 females; Table S2) participated in Experiment 2.
121 Experiment 2 consisted of eight trials, each involving a demonstration phase and a choice phase
122 (Figure 3; Movie S3) modeled after a similar social preference task [33]. In the demonstration
123 phase, subjects watched as a neutral actor dropped a toy out of reach, a helper retrieved the toy
124 and attempted to return it to the neutral actor, and a hinderer prevented the transfer by
125 aggressively snatching the toy. In the choice phase, which followed immediately, the helper and
126 hinderer approached the bonobo simultaneously with a piece of apple in their hand. Subjects
127 received food from whichever actor they approached first.

128 Overall, subjects tended to select the hinderer more frequently than the helper
129 ($M=0.551\pm 0.036$ of trials), but not significantly above chance [$N=22$, $p=0.158$; Figure 2B]. Since
130 in Experiment 1 only adults exhibited a hinderer preference, we again separated our sample into
131 adults and subadults, replicating the age-dependent pattern. Adults, but not subadults, exhibited a
132 significant preference for the hinderer [adults: $N_{aged9-17}=14$, $M=0.607\pm 0.047$, $p=0.047$; subadults:
133 $N_{aged4-8}=8$, $M=0.453\pm 0.040$, $p=0.257$; Figure 2B], extending the Experiment 1 finding to a
134 completely different real world context.

135 In Experiment 3, we further tested the robustness of adult bonobos' preference for
136 hinderers by replicating Experiment 2 but including an additional baseline phase to assess and
137 control for subjects' arbitrary preferences for the experimenters. Experiment 3, therefore, tested
138 whether bonobos would shift their initial preference toward the hinderer once he began to behave
139 antisocially.

140 Experiment 3 employed identical methods to Experiment 2 (Figure 3), except subjects
141 participated in four baseline trials before completing four test trials ($N=18$ adult bonobos, ages
142 10-18, 9 females; Table S3) [see 34 for a similar design]. Baseline trials only involved the choice
143 phase of the procedure from Experiment 2, while test trials included the demonstration and
144 choice phases. Additionally, after making their choice, subjects did not receive food from either
145 experimenter. If subjects approached one experimenter during the majority of baseline trials, this
146 experimenter was assigned the role of helper. If subjects approached the experimenters equally
147 during baseline trials, roles were assigned semi-randomly, with the aim of counterbalancing the
148 role played by each experimenter across subjects [34].

149 Bonobos exhibited a significant shift between the baseline and test phases in response to
150 the social demonstrations [related-samples Wilcoxon signed rank test: $N=18$, $p=0.032$; Figure
151 2C]. Specifically, 10 of 18 individuals shifted from their baseline preference toward the hinderer,
152 and only 3 exhibited the opposite shift. Taken together, these three experiments demonstrate that
153 bonobos have a robust preference for individuals that behave antisocially over those that behave
154 prosocially toward others.

155 **Experiment 4: Bonobos prefer animated agents that are dominant**

156 In Experiment 4, we further tested the dominance hypothesis—that subjects' hinderer
157 preference might be explained by an attraction to individuals perceived as dominant, since

158 dominant individuals may be the most desirable allies or social partners. Although in principle
159 prosocial and antisocial individuals can be dominant or subordinate, antisocial behavior is often
160 used to establish and maintain dominance and the specific antisocial behaviors exhibited by
161 hinderers in our studies and those with human infants resemble dominance interactions: the
162 hinderer prevails over the neutral agent or the helper in reaching his goal (of descending the hill
163 or acquiring the toy) [35-37]. Therefore, according to the dominance hypothesis, we predicted
164 that bonobos would exhibit a preference for an antisocial dominant over a subordinate as they
165 did for hinderers over helpers.

166 Experiment 4 was identical to Experiment 1, except for the animations ($N=24$, ages 4-17,
167 10 females; Table S4). In the test session (Movie S4), subjects watched a video in which two
168 animated agents competed for access to a central location in the scene, with the dominant agent
169 repeatedly displacing the subordinate one, a dominance interaction familiar to nonhuman
170 primates (see also seminal work with humans by Heider and Simmel [38]). To ensure that a
171 preference in the test session did not stem from perceptual features, in the control session (Movie
172 S4) subjects witnessed the same video (with new agents) except that the agents' actions were
173 separated in time such that they were no longer contingent and therefore the agents should not be
174 perceived as being dominant or subordinate to one another. As in Experiment 1, all subjects
175 participated in both conditions on separate days, with condition order counterbalanced across
176 individuals.

177 Subjects exhibited a significant preference for the dominant agent [$N=24$,
178 $M=0.604\pm 0.033$, $p=0.008$; Figure 2D]. No subjects chose the subordinate on a majority of trials
179 while eight favored the dominant. In the control, bonobos showed no preference for either agent
180 [$N=24$, $M=0.531\pm 0.023$, $p=0.180$; Figure 2D]. One favored the subordinate control and four the

181 dominant control. Within-subject comparisons revealed that subjects selected the dominant agent
182 significantly more than its control counterpart [related samples Wilcoxon signed rank test, $N=24$,
183 $p=0.035$; Figure 2D]. When the sample was split into adults and subadults, the effects replicated
184 only in adults, although the subadult sample size was notably smaller ($N=6$; see Supplemental
185 Information). Given that bonobos' dominance preference is driven by eight subjects, it's possible
186 that this effect explains some but not all of the preference for hinderers documented in the first
187 three experiments.

188

189 **DISCUSSION**

190 Our results support the predictions of the dominance hypothesis and raise the possibility
191 that the motivation to prefer prosocial individuals evolved in humans after their divergence from
192 the other apes. In three experiments, adult bonobos spontaneously chose a human or animated
193 agent that hindered another individual over one that helped. In contrast, by three months of age,
194 human infants already show the *opposite* preference in related paradigms [6-8]. Bonobos failed
195 to show a human-like preference despite their relative tolerance and prosociality in dyadic
196 interactions [11, 15]. However, bonobos were sensitive to the actors' goal-directed actions
197 towards others, clearly discriminating between helpers and hinderers, even when they were just
198 animated shapes with eyes. This finding suggests that bonobos do track interactions between
199 third-parties and evaluate potential social partners based on these interactions [39, 40].

200 Our main finding is reproducible, having replicated in three different experiments,
201 involving multiple paradigms with both humans and animated agents as actors. Our experiments
202 controlled for attraction to different colors, shapes, or motion patterns. Agent color and shape
203 were counterbalanced between subjects and, when key social features were removed, bonobos

204 showed no preference for control agents that exhibited similar motion patterns. The fact that
205 bonobos showed consistent preferences across all of our studies also provides validation for the
206 more artificial but completely novel animation-based experiments. By using non-differential or
207 zero rewarding and few trials, subjects did not have an opportunity to form preferences based on
208 food acquisition. Moreover, our use of both novel animated agents and unfamiliar human
209 experimenters allowed us to eliminate biases in social preference based on social information
210 that is unrelated to the goals of our study (such as sex, age, reproductive status, and size of the
211 agents). Critically, bonobos' preferences were tested in a context that differed from the one in
212 which the actors' prosocial and antisocial behavior was demonstrated, minimizing the possibility
213 that, at the moment of choice, subjects were simply expecting to be able to use the actor as a
214 context-specific social tool.

215 Although the results of Experiment 1 could be interpreted as bonobos preferring to steal
216 food from the hinderer (since food accompanied their choices), Experiments 2-4 suggest that this
217 was not the case. For one, this interpretation would suggest that, in Experiment 4, bonobos also
218 preferred to steal from a dominant, which is antithetical to the concept of dominance and thus
219 unlikely. Moreover, Experiments 2 and 3 were based on a paradigm in which bonobos preferred
220 to approach an individual who had recently groomed or played with them over one who had not
221 [34], suggesting that these measures reflect social affinity rather than acts of punishment. Finally,
222 the interpretation that bonobos prefer dominant hinderers accords with natural observations in
223 which bonobos exhibit courtesy begging toward high-ranking individuals to build and test
224 relationships [16].

225 Bonobos may prefer hinderers because they appear to be more dominant than helpers.
226 When intervening in third-party conflicts, primates often support the higher-ranking contestant or

227 the one who is already winning (i.e., “winner-support”), and they may gain reproductive benefits
228 from doing so [24, 41]. For example, high-ranking male chimpanzees, who often prevent others
229 from mating, have been shown to be more tolerant of mating by their supporters [42]. In food
230 sharing contexts, wild bonobos preferentially beg for food from dominants even when they can
231 easily obtain the same food themselves, perhaps to test their social tolerance [16]. Recent
232 evidence also suggests that female bonobos may exert especially high levels of choice in mating
233 decisions, selecting the highest-ranking males [43]. In support of this dominance preference
234 interpretation, in Experiment 4, bonobos favored a dominant agent over a subordinate one.
235 Hindering and dominance are not inextricably linked, however, and, as such, research with
236 humans and nonhuman animals should continue to investigate understanding of these qualities
237 and the relationship between preferences for prosocial versus antisocial agents and for dominants
238 versus subordinates.

239 Future work should also examine whether there are contexts in which bonobos do prefer
240 prosocial individuals (e.g. in response to conspecifics). Our spontaneous measures can also be
241 extended to a range of species. Capuchin monkeys (*Cebus apella*) would be a good prospect
242 since in some contexts they show a preference for helpers over non-helpers. However, they have
243 yet to be tested for their preference between helpers and hinderers [44]. Our work will also need
244 to be extended to other apes to provide more resolution on the phylogenetic history of this trait in
245 our lineage. For example, chimpanzees and orangutans spontaneously requested food from a
246 human they had observed sharing food with a third-party over one who had refused to share [26-
247 28]. However, it is unclear whether this potential prosocial preference would generalize to cases,
248 like those investigated in our experiments and experiments with human infants, where
249 participants must evaluate others based on prosocial and antisocial interactions that are not

250 immediately relevant to the participants. Chimpanzees prefer to seek food from an individual
251 who has shared food moments before, but would they also prefer to interact with an individual
252 who has previously helped a third-party to access a goal object, as human infants do, or would
253 they instead prefer to interact with someone who has previously thwarted a third-party's goal,
254 like bonobos? Further work on chimpanzees' social preferences and evaluative cognition is
255 necessary to clarify whether bonobos or humans show the more derived preference.

256 Regardless of what future research reveals about the motivations underlying social
257 preference in human infants and their closest bonobo relatives, the current study demonstrates
258 that in nearly identical settings the two species exhibit *very* different preferences. Thus, while
259 nonhuman apes possess the cognitive architecture to track third-party interactions and flexibly
260 evaluate others as social tools [25-28], there currently remains little evidence that they positively
261 evaluate partners based on their prosocial dispositions toward others. Therefore, an early-
262 emerging preference for those that are prosocial toward others may be among the species-
263 specific traits at the foundation of humans' uniquely cooperative nature.

264

265 **Author Contributions**

266 C.K. and B.H. designed the experiments, analyzed the data, and wrote the paper. C.K. collected
267 the data.

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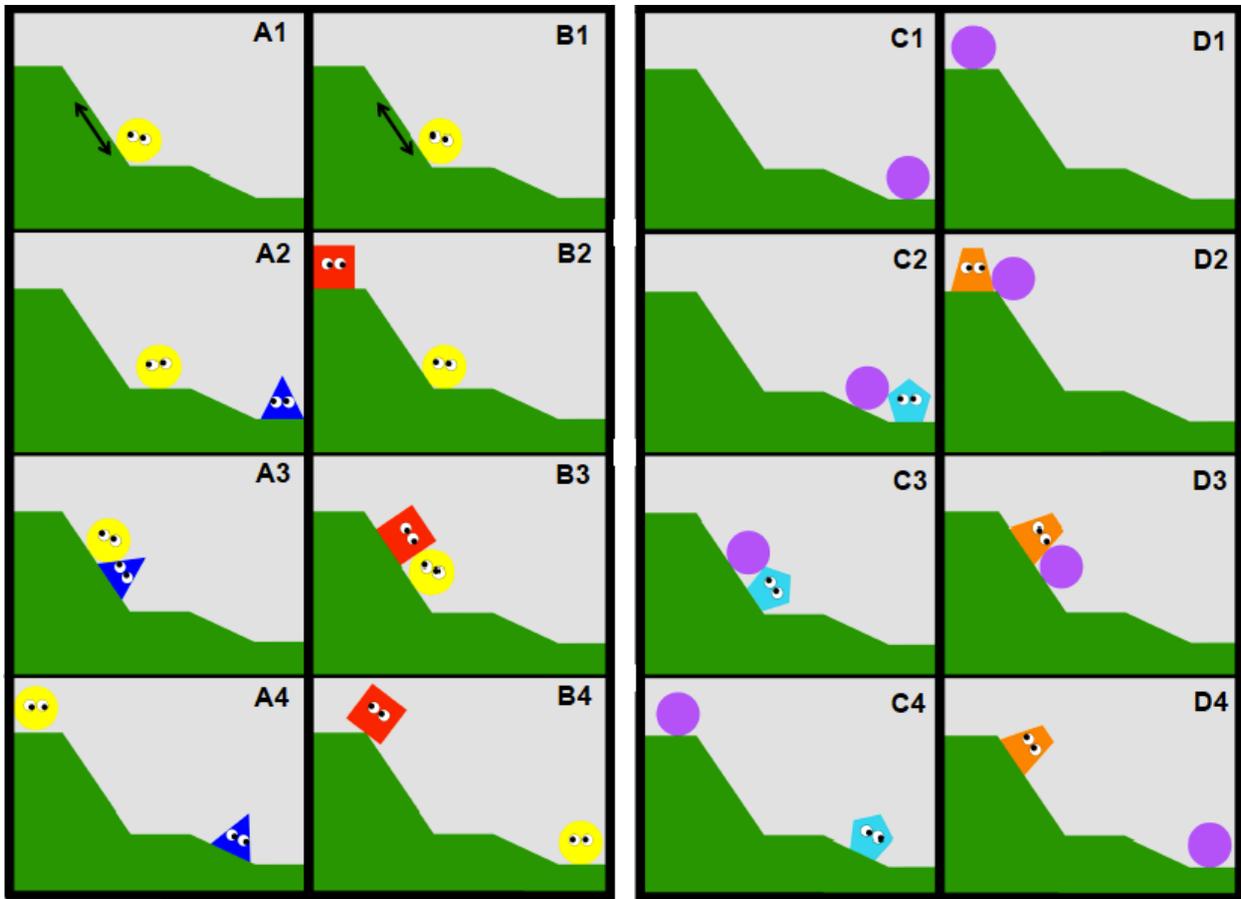
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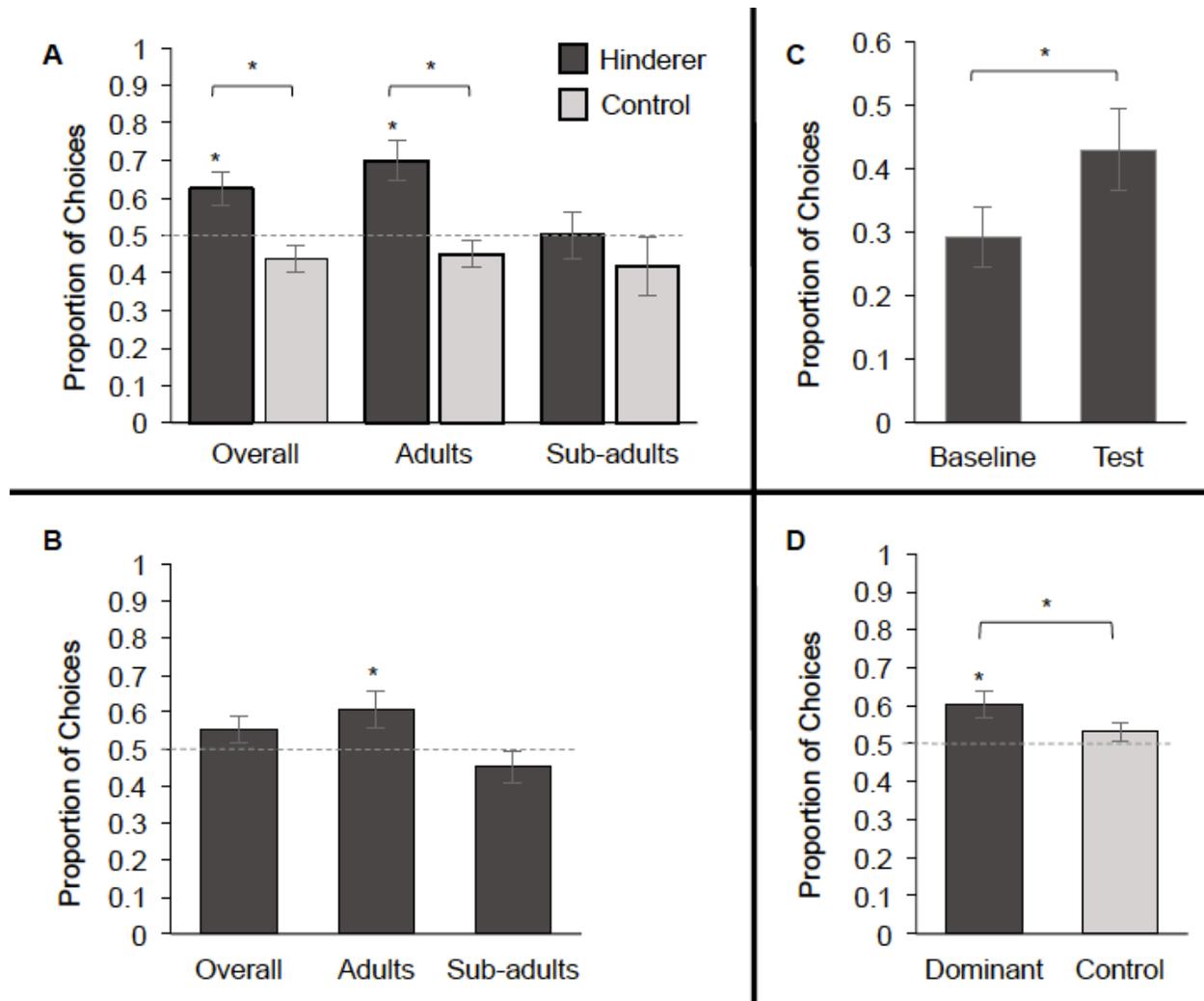
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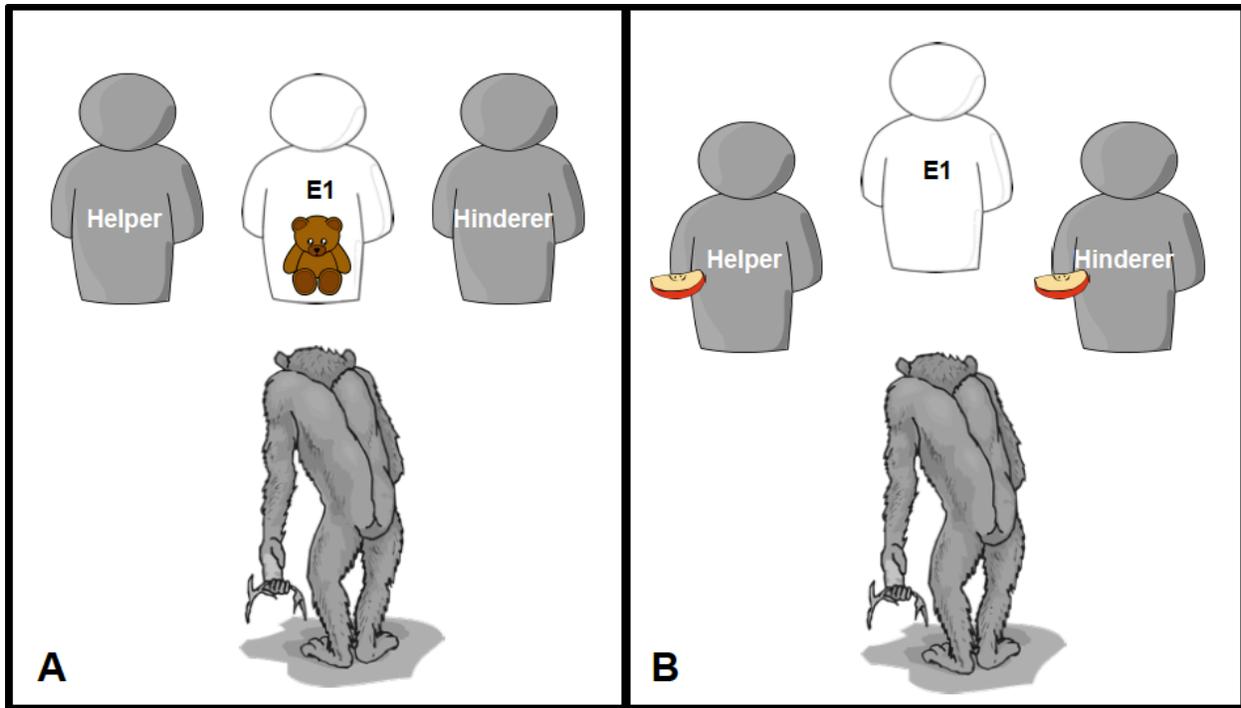
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415 **Figure 1. Frames from Experiment 1 video stimuli. A. Helper animation. B. Hinderer**
 416 **animation. C. Upward animation. D. Downward animation** In both the helper (A) and
 417 hinderer (B) animations, the climber (yellow circle) tries but fails to scale the hill (A1 and B1)
 418 three times before encountering another agent. In the *helper animation*, the helper (blue triangle)
 419 enters from below (A2), pushes the climber up the hill (A3), and exits the screen (A4). In the
 420 *hinderer animation*, the hinderer (red square) enters from above (B2), pushes the climber down
 421 the hill (B3), and exits the screen (B4). The *upward animation* (C) begins with a static ball at the
 422 base of the hill (C1). The upward agent enters from below (C2), pushes the ball up the hill (C3),
 423 and exits the screen (C4). Conversely, the *downward animation* (D) begins with a static ball at
 424 the top of the hill (D1). The downward agent enters from above (D2), pushes the ball down the
 425 hill (D3), and exits the screen (D4). See also Movies S1 and S2 and Table S1.



426

427 **Figure 2. Results of Experiments 1-4.** A. Mean proportion of choices for the hinderer and
 428 control in Experiment 1, overall and for adults and sub-adults. B. Mean proportion of choices for
 429 the hinderer in Experiment 2, overall and for adults and subadults. C. Shift in proportion of
 430 choices for the hinderer between baseline and test in Experiment 3. D. Mean proportion of
 431 choices for the dominant and control in Experiment 4. Asterisks indicate significant effects ($p <$
 432 0.05). Error bars depict standard error. See also Tables S1-4.



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Figure 3. Experimental procedure of Experiments 2 and 3. A. Demonstration. Subjects watched as E1 played with and ultimately dropped a stuffed animal out of reach. The helper retrieved the toy and attempted to return it to E1, until the hinderer intervened and aggressively stole the toy. B. Choice phase. Subjects could approach either the helper or hinderer, both of whom held a piece of apple in their outstretched hand. See also Movie S3 and Tables S2 and S3.

Subject	Sex	Age		Exp. Participation
		Exp. 1	Exp. 2-4	
Api*	M	12	15	1 & 3
Bandundu*	F	15		1
Bili*	M	11	14	1 & 3
Bisengo	M	7		1
Boma	F		4	2 & 4
Chibombo	M		10	2-4
Dilolo*	M	11	14	1-4
Eleke	M		12	3 & 4
Elikiya	F		10	3
Fizi*	M	12		1
Ilebo*	M		14	2 & 4
Kalina*	F	14	17	1, 2, & 4
Kananga	F	5	8	1, 2, & 4
Kasongo*	M	10	13	1, 2, & 4
Katako	F	8	11	1-4
Kikwit*	M	15	17	1, 2, & 4
Kinshasa	F		10	2-4
Kinzia	F		4	2
Kisantu	F	14		1
Kodoro	M		8	2
Kole	M		9	4
Likasi*	F		14	2
Lisala*	F	11		1
Lomako	M		8	2 & 4
Lomami*	M	13	16	1-3
Lukuru	F		10	2-4
Mabali*	M		14	3 & 4
Malaika	F	5	8	1 & 2
Masisi	F	7	10	1, 3, & 4
Matadi*	M	11	14	1, 3, & 4
Maya	F	19		1
Mbandaka*	M		14	2
Moyi	M		8	2 & 4
Muanda	F		12	3 & 4
Opala*	F	7		1
Oshwe	M	4	7	1 & 4
Pole	M	6		1
Sake	F	7		1
Salonga*	F		18	3
Sandoa	F		10	2-4
Singi	M		6	2 & 4
Waka	F	7	10	1-4
Yolo*	M	9	12	1, 3, & 4

439
440 **Table 1. Subject characteristics and participation in experiments 1-4.** For sex, ‘M’ refers to
441 males and ‘F’ to females. Age refers to age estimate in years. Asterisks denote subjects tested by
442 Herrmann, et al. [26].

443 **STAR Methods:**

444 **CONTACT FOR REAGENT AND RESOURCE SHARING**

445 Further information and requests for resources should be directed to and will be fulfilled by the
446 Lead Contact, Christopher Krupenye (ckrupenye@gmail.com).

447

448 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

449 Forty-three semi-free-ranging bonobos (aged 4-19; 21 females; see Table 1) were tested at Lola
450 ya Bonobo sanctuary in Kinshasa, Democratic Republic of Congo (www.friendofbonobos.org)
451 during two field seasons (October-December, 2012: Experiment 1; May-June, 2015:
452 Experiments 2-4; see Table 1). Animal husbandry and care practices complied with the Pan-
453 African Sanctuary Alliance (PASA) Primate Veterinary Healthcare Manual, as well as the
454 policies of Lola ya Bonobo Sanctuary. These non-invasive behavioral studies were approved by
455 Duke University IACUC (A035-14-02) and adhered to host country laws. Apes in African
456 sanctuaries are typically born in the wild, and enter the sanctuary after being confiscated at an
457 early age (~2-3 years old) as a result of the trade in wildlife for pets and bushmeat. Previous
458 work indicates that sanctuary apes are psychologically healthy relative to other captive
459 populations [45]. All subjects were socially housed, and free-ranged in large tracts of tropical
460 forest during the day (5-40 hectares across groups). In the evening, all apes spent the night in
461 indoor dormitories (12 m²-160 m²). Apes were tested individually in these familiar dormitory
462 buildings. Following testing, all subjects were released back with their larger social groups
463 outside. Subjects had ad libitum access to water and were not food-restricted during testing. In
464 addition to food naturally available in their forest enclosures, apes were fed a variety of fruits,
465 vegetables, and other species-appropriate foods two to four times daily. Apes were tested on only

466 one session per day and all tests were voluntary. If apes refused to approach the experimenters
467 and participate in the studies or if they became upset (e.g., screaming, banging), they were
468 released from the testing room. In Experiments 1 and 4, if a subject did not make a choice within
469 five minutes, the session was aborted and the subject excluded from analyses (one subject in
470 Experiment 4). In Experiments 2 and 3, if a subject did not make a choice within one minute, the
471 trial was repeated. If the subject did not make a choice for more than three trials, the session was
472 aborted and the subject was excluded from any analyses (two subjects in Experiment 2 and eight
473 in Experiment 3). In addition, one subject, who was small enough to reach his entire arm through
474 the bars (instead of just his fingers), was excluded from Experiment 1 for repeatedly disrupting
475 the experimenter's attempts to present the choices and ultimately making it impossible for the
476 experimenter to test him. One subject was excluded from Experiment 2 due to experimenter error
477 (i.e., failing to correctly counterbalance experimenter locations across trials).

478

479 **METHOD DETAILS**

480 **Experiment 1**

481 *Procedure*

482 Subjects were tested alone in a testing room. The experimenter positioned himself at a
483 small table just outside of the testing room, across the mesh from the subject. The experimenter
484 presented video stimuli to the subjects via an iPad and then allowed subjects to choose between
485 paper cutouts of animated agents from the videos (Movies S1 and S2). Importantly, previous
486 work has demonstrated that apes can treat animated agents as goal-directed [29], track the goals
487 and third-party interactions of agents on screens [46-48], have some understanding of iconic

488 representation [49, 50], equate 2-D depictions in video with real life objects [51], and treat
489 images of familiar individuals on a monitor as representative of those individuals [52, 53].

490 In both test and control sessions (which occurred on separate days, with order
491 counterbalanced between subjects), subjects were first familiarized to the relevant animations on
492 the iPad (i.e., test session: helper and hinderer animations; control session: upward and
493 downward animations) as they alternated in a loop for a total of four presentations of each
494 animation. To begin presentation of the animations, the experimenter attracted the subject's
495 attention by calling her name and began the video sequence, shifting the direction of the iPad to
496 maximize viewing in cases where the subject moved or shifted her gaze. Additionally, subjects
497 who moved to the back of the room (i.e., away from the iPad) or looked away from the iPad for
498 more than several seconds were offered small pieces of food to regain their attention.

499 Four test trials were conducted immediately following familiarization. Before being
500 given a choice in each test trial, subjects again watched both animations once (order
501 counterbalanced within-subjects). After the experimenter finished showing the animations, he
502 either moved the table so that the subject was sitting at the midline of the table or used a piece of
503 food to attract the subject to that central location. This process ensured that during the choice
504 phase, subjects had equal access to both options. The experimenter then simultaneously placed
505 two pieces of apple on the middle of the table, held up 5cm² cutouts of the two agents (i.e., test
506 session: helper and hinderer; control session: upward and downward agents) above the pieces of
507 apple for 2 seconds, laid them on top of the pieces of apples, moved the agents (and now
508 occluded apples) to opposite sides of the table, pushed the sliding table-top forward to allow the
509 subject to make a choice, and started a stop watch. To make a choice, subjects gestured toward
510 one of the agents (i.e., protruding her finger through the mesh to touch the agent). Once the

511 subject had made a choice, she was provided the paper cutout and associated apple. The other
512 agent and apple piece were removed from the table. If a subject double-pointed (i.e., used both
513 hands to select both options at the same time) or did not make a choice within a minute, the
514 experimenter pulled the table back, and waited a few seconds before presenting the choice again.
515 To avoid influencing the subject's choice, all actions involved in presenting the choices occurred
516 simultaneously, the locations of the helper and hinderer replicas (or upward and downward
517 controls) were counterbalanced across trials, and the experimenter looked directly at the subject
518 while pushing the table forward and waiting for the subject to make a choice [32].

519 *Design*

520 All bonobos participated in both the test and control conditions, but at least two days
521 elapsed between sessions. Half of subjects began with the test condition and half the control.
522 Animated events were made on Adobe Flash Professional CS6. To control for any individual
523 preferences for shape or color, four pairs of agents were created: red square and blue triangle,
524 blue square and red triangle, orange pentagon and aqua trapezoid, and aqua pentagon and orange
525 trapezoid. Each subject witnessed different agent pairs in test and control conditions that did not
526 share any physical characteristics with each other (e.g. if the test agents were red square and blue
527 triangle, the control agents could be orange pentagon and aqua trapezoid or aqua pentagon and
528 orange trapezoid, but not blue square and red triangle). Agent pairs were assigned to subjects at
529 equal frequency and the role of each agent as the helper, hinderer, upward agent, and downward
530 agent was counterbalanced across subjects. The pair of agents assigned to a subject remained
531 constant throughout the session.

532 To control for the fact that the helper and upward agent enter from the opposite side of
533 the scene as the hinderer and downward agent, we created mirrored versions of all videos. For

534 each subject, half of the presentations of each video were the original version and half were the
535 mirrored version. We counterbalanced the order of original versus mirrored presentations within
536 and between subjects and we counterbalanced which occurred on the first trial between subjects.

537 Since during the familiarization phase, the video type (e.g., helper video or hinderer
538 video) alternated four times (e.g., helper, hinderer, helper, hinderer, helper, hinderer, helper,
539 hinderer), we counterbalanced between subjects which video was shown first. We also
540 counterbalanced within and between subjects which video played first during test trials.

541 *Scoring*

542 Choices were live-scored by the experimenter. All tests were videotaped, and a second
543 coder blind to conditions and hypotheses scored 100% of sessions with excellent reliability
544 [99.0% agreement, Cohen's kappa = 0.979]. Specifically, to ensure that the coder was blind, we
545 renamed all videos with a number and told the coder to review the videos with the sound turned
546 off. Since the vantage point of the video did not allow the coder to see the media displayed to the
547 bonobo on the iPad, there was no way that he could have inferred the condition or the roles of the
548 agents.

549 **Experiment 2**

550 Subjects participated in a series of eight trials in a single session. Each trial consisted of a
551 demonstration phase followed by a choice phase (Movie S3). In the demonstration phase, a pair
552 of experimenters sat on either side of a third neutral actor (E1) just outside the subject's
553 enclosure. These experimenters (the helper and hinderer) were two Congolese men of similar age
554 who were familiar with the sanctuary but had never interacted with the bonobos. Their roles were
555 counterbalanced across subjects. E1 was playing with a plush toy, tossing it in the air and
556 mimicking bonobo laughter, when he dropped the toy out of reach and then grasped for it

557 effortfully—vocalizing and gazing at it with arm outstretched. The helper calmly picked up the
558 toy, made eye contact with E1, and attempted to return the toy to E1. Before E1 could take the
559 toy, the hinderer snatched the toy from the helper, aggressively grunted, and turned his back to
560 the other two, surreptitiously depositing the toy in a bucket between himself and E1. As a
561 familiarization, subjects first watched the demonstration two times (and then a third time as part
562 of the first trial) to ensure that by the first choice phase they were familiar with the behavior of
563 each experimenter. E1 then said, “ok,” and the three stood up with their backs to the subject,
564 beginning the choice phase. E1 gave the helper and hinderer a piece of apple, made sure the
565 experimenters were roughly 1m apart, positioned the bonobo centrally with an additional piece
566 of food, and then directed the experimenters to simultaneously turn toward the bonobo and
567 approach her with the food in their outstretched hands. When the experimenters arrived, E1
568 started a stopwatch and the bonobo had one minute to choose between the experimenters. A
569 choice was made if the subject approached one experimenter and gestured toward the food with
570 her hand or mouth (i.e., put her hand or mouth up to the mesh where the experimenter held the
571 food). She was then given the piece of apple by the experimenter she chose. All experimenters
572 then turned around and the unchosen experimenter’s food was placed in the bucket. The
573 experimenters sat in the appropriate location for the next trial’s demonstration phase, which
574 began immediately.

575 *Design*

576 The roles of the experimenters remained constant for a given bonobo, but were
577 counterbalanced across subjects. We counterbalanced the locations of the helper and hinderer
578 across trials (i.e., which experimenter was positioned to the left and which to the right of E1).
579 Half of the subjects experienced ABBABAAB order while the other half experienced

580 BAABABBA order. Experimenters remained in the same location for the demonstration and
581 choice phases of a given trial. During the two familiarization demonstrations that preceded the
582 first trial, experimenters occupied the positions assigned to them for the first trial.

583 *Scoring*

584 E1 live-scored the subject's choices. A second coder, blind to hypotheses and
585 experimental manipulation (i.e. the experimenters' roles), reviewed video footage of 23% of
586 trials and coded subjects' choices for reliability, achieving excellent agreement (100%
587 agreement, Cohen's kappa = 1.0). Coders recorded which experimenter (Left or Right) the
588 subject selected first.

589

590 **Experiment 3**

591 *Procedure and Design*

592 The procedure and design of this study were identical to that of Experiment 2, except for
593 three key differences. First, we altered the choice phase of the task. Although the helper and
594 hinderer still held out a piece of apple to the bonobo, this food was not given to the subject after
595 she made her choice. That is, the helper and hinderer never provisioned the subject; the subject
596 only received food from E1, the neutral actor. Second, test trials were preceded by four baseline
597 trials to measure any pre-existing preferences for the experimenters. Baseline trials involved only
598 the choice phase from Experiment 2. If the subject demonstrated a preference for one
599 experimenter during baseline trials (i.e., choosing him three or four times), that experimenter was
600 assigned to the role of the helper and the less-preferred experimenter was assigned the role of
601 hinderer. If the subject chose each experimenter twice, the experimenters were assigned to their
602 roles pseudo-randomly, based on the goal of counterbalancing each experimenter's roles across

603 subjects. Finally, subjects only participated in four instead of eight test trials (following the four
604 baseline trials). As in Experiment 2, subjects witnessed the demonstration three times before the
605 choice phase of the first test trial, and one additional time before the choice phase of each of the
606 other test trials. Locations of the experimenters were counterbalanced across trials, with the same
607 order repeated in both baseline and test trials for a given subject. Half of subjects experienced
608 ABBA order and the other half BAAB order.

609 *Scoring*

610 Again, E1 live coded subjects' choices and a second reliability coder blind to hypothesis
611 and experimenters' roles coded 22% of trials, using the same choice criteria as Experiment 2.
612 Agreement was excellent (100% agreement, Cohen's kappa = 1.0).

613

614 **Experiment 4**

615 *Procedure and Design*

616 The procedure and design of Experiment 4 were identical to those of Experiment 1, save
617 for the use of different animations. In addition, rather than witnessing two separate animations,
618 showcasing the behavior of each agent (e.g., like the helper and hinderer animations), in
619 Experiment 4, each condition featured a single animation depicting interactions between the two
620 agents. The test animation featured a dominant agent and a subordinate agent engaging in a
621 dominance contest (Movie S4). In the animation, the subordinate moved to a contested location
622 and was displaced several times by the dominant agent. That is, each time that the subordinate
623 moved to the contested location, the dominant appeared quickly, pushed the subordinate off of
624 the spot, and returned to occupy the location briefly. Eventually the dominant moved from the

625 contested location. Once the dominant arrived at its rest location, the subordinate then slowly
626 inched back to the contested location before being displaced again by the dominant.

627 To ensure that subjects' choices did not reflect preferences for a motion pattern rather
628 than for the social content of the video, the control animation involved identical movements as
629 those in the test but the contingency between the agents' actions was removed. That is, the first
630 agent moved to and then away from the contested location before the second agent moved to and
631 away from the same location. As in Experiment 1, the shapes and colors of the agents were
632 counterbalanced such that for a given subject each role (i.e., dominant, subordinate, control
633 dominant, control subordinate) was occupied by a different agent, but across subjects each agent
634 was used equally for each role. As in Experiment 1, we controlled for unintentional cueing by the
635 experimenter by coordinating placement of apple pieces and agents on the left and right at the
636 exact same time, sliding the options forward at the exact same time using a sliding table top, and
637 having the experimenter look toward the center of the table while placing the objects and look
638 toward the ape while pushing the table forward.

639 *Scoring*

640 E1 live scored subjects' choices and a second coder, blind to condition, role of the agents,
641 and hypotheses, coded 100% of trials, using the same criteria for marking a choice as
642 Experiment 1. Agreement was excellent (100% agreement, Cohen's kappa = 1.0).

643

644 **QUANTIFICATION AND STATISTICAL ANALYSIS**

645 Proportions of choices for the hinderer (Experiments 1-3), downward agent [i.e., hinderer
646 control] (Experiment 1), dominant (Experiment 4), and dominant control (Experiment 4) were
647 calculated for each subject. Analyses of bonobos' preferences within and between conditions

648 (two-tailed one sample and related samples Wilcoxon signed rank tests) and calculation of
649 reliability on coding (Cohen's Kappa) were performed using SPSS, version 23.

650 To test whether humans are precocious relative to our closest relatives in the
651 development of third-party social evaluation, we examined the relationship between age and
652 social preference in bonobos. We split our subjects into adults and subadults, using a relatively
653 conservative measure of maturity. Although in the wild bonobo females disperse from their natal
654 group by ten years of age, individuals at Lola ya Bonobo sanctuary begin to reach sexual
655 maturity at the very earliest at age 8 [15, 54]. Therefore, for developmental analyses, we grouped
656 individuals 9 and above into our adult cohort and those 8 and below into our subadult cohort.

657

658 **Experiment 1**

659 *Unintentional Cueing Check*

660 As an additional precaution to ensure that subjects' choices were not influenced by
661 unintentional cueing in the experimenter's presentation of the choices in the test phase, two
662 additional coders blind to condition and the role of each agent reviewed the videos to determine
663 if during the presentation of choices in either experiment the experimenter had placed either
664 choice closer to the edge of the table, or stopped moving one choice earlier than the other.
665 VirtualDub was used to allow coders to view the experimental videos frame by frame (30
666 frames/second). For each trial, coders skipped to a time when both options had been presented
667 but before the subject had made a choice. To test whether E subconsciously placed the agents in
668 a manner that might encourage the choice of one agent over the other simply because it was
669 slightly closer to the subject, coders recorded whether one agent was placed closer to the edge of
670 the table than the other. Visibility in videos permitted this "moved closer" coding in 190 of 192

671 trials. To test whether E subconsciously placed the agents in a manner that might encourage the
672 choice of one agent over the other simply because the movements of the two agents ended at
673 slightly different times, coders watched frame by frame in reverse, recording the frame for the
674 moment when each hand first moved the agent. Watched forward this is the hand's final
675 movement of the agent to its final choice location. One agent was considered to have stopped
676 moving perceptibly earlier than the other if the difference between the left and right hands' final
677 movement times was greater than 6 frames (200 ms) since this is the minimum time differential
678 nonhuman apes need to perceive events [55]. Visibility in videos permitted this "moved later"
679 coding in 182 of 192 trials. Reliability on these measures was substantial [56] [moved closer:
680 91.1% agreement, Cohen's kappa = 0.767; moved later: 95.6% agreement, Cohen's kappa =
681 0.754].

682 To determine if unconscious movement measures contributed to our results, we
683 reanalyzed the data from Experiment 1, excluding the trials on which both coders agreed that one
684 agent was moved closer (35 trials) or moved later (14 trials). In both cases, we replicated our
685 findings in the test condition: subjects exhibited a significant preference for the hinderer [one
686 sample Wilcoxon signed rank tests: moved closer trials excluded: $N = 23$, $p = 0.013$; moved later
687 trials excluded: $N = 24$, $p = 0.015$]. Reanalysis of the control condition revealed that with moved
688 closer trials excluded subjects had a preference for the upward bound agent [$N = 24$, $p = 0.043$],
689 the agent whose motor patterns mirrored the helper, not the hinderer, and with moved later trials
690 excluded subjects had no preference for either agent [$N = 24$, $p = 0.114$]. We also replicated our
691 finding that subjects' choices in the test condition were significantly different from their patterns
692 of choice in the control [related samples Wilcoxon signed rank tests: moved closer trials
693 excluded: $z = -2.833$, $N = 23$, $T+ = 3$, ties = 4, $p = 0.005$; moved later trials excluded: $z = -2.913$,

694 $N = 24$, $T+ = 3$, ties = 8, $p = 0.004$]. These results suggest that subjects' selection of the hinderer
695 in the test condition cannot be accounted for by a preference for the agent's motor pattern, and
696 that presentation of one agent closer or later than the other is unlikely to have influenced our
697 findings.

698 *Developmental Analyses*

699 Like the population overall, adults ($N = 15$; aged 9-19; 6 females) exhibited a robust
700 preference for the hinderer [one-sample Wilcoxon signed rank test, $N = 15$, $p = 0.006$] but no
701 preference in the control condition [$N = 15$, $p = 0.180$], and chose the hinderer significantly more
702 frequently than the downward agent [related samples Wilcoxon signed rank test, $z = -2.719$, $N =$
703 15 , $T+ = 9$, ties = 6, $p = 0.007$]. Subadults ($N = 9$; aged 4-8; 6 females), however, showed no
704 preference in the test [$N = 9$, $p = 1.000$] or control [$N = 9$, $p = 0.257$], and no difference in choice
705 patterns between conditions [$z = -1.000$, $N = 9$, $T+ = 4$, ties = 3, $p = 0.317$]. Further, there was a
706 significant difference in choice patterns between the older and younger cohorts in the test [Mann-
707 Whitney U test: $U = 33.000$, $z = -2.211$, $N_{\text{age } 4-8} = 9$, $N_{\text{age } 9-19} = 15$, $p = 0.027$] but not in the
708 control [Mann-Whitney U test: $U = 61.000$, $z = -0.510$, $N_{\text{age } 4-8} = 9$, $N_{\text{age } 9-19} = 15$, $p = 0.610$].
709 These results suggest that social preference may not emerge in bonobos until maturity, and that
710 there may have been a shift in the ontogeny of this trait since humans and bonobos diverged.
711 Studies with chimpanzees are necessary to more confidently infer whether bonobos are
712 developmentally delayed, or humans precocious, relative to the ancestral condition.

713 *Within-Session Analyses*

714 To assess how quickly bonobos formed their preferences we examined their choices on
715 the first trial. Subjects did not show a first trial preference for either agent in the test [Binomial
716 test, $N = 24$, $p = 1.000$] or control [Binomial Test, $N = 24$, $p = 0.064$], and showed no difference

717 between conditions [Wilcoxon signed rank test, $z = -1.508$, $N = 24$, $T+ = 8$, ties = 13, $p = 0.132$].
 718 For each condition, we then compared subjects' preferences in the first half of the session with
 719 that of the second half. There were no differences in choice patterns between the first and second
 720 half of the test [Wilcoxon signed rank test, $z = -0.443$, $N = 24$, $T+ = 6$, ties = 11, $p = 0.658$] or
 721 control conditions [Wilcoxon signed rank test, $z = -0.707$, $N = 24$, $T+ = 2$, ties = 19, $p = 0.480$],
 722 indicating that subjects' choices (i.e., preference for the hinderer and no preference among
 723 upward/downward agents) were consistent throughout each session.

724

725 **Experiment 2**

726 *Order Effects*

727 Ideally, our studies would involve unique subjects. However, this was not possible as
 728 bonobos are a highly endangered species endemic only to the Democratic Republic of Congo.
 729 Even accessing the largest sample of bonobos in the world (at Lola ya Bonobo, DRC), some
 730 subjects had to be tested in multiple studies (Table 1) to maximize sample size. To investigate
 731 whether participation in one study could influence performance on the next (and to ensure that
 732 foods received for subjects' choices in Experiment 1, which were predominantly choices of the
 733 hinderer, could not explain the results of subsequent experiments), we compared the mean choice
 734 of the hinderer in Experiment 2 between subjects who had participated in Experiment 1 and
 735 those who had not. Overall, naïve subjects ($M=0.596$) showed a slightly higher tendency to
 736 choose the hinderer than experienced subjects ($M=0.486$), although this difference was not
 737 significant [Mann-Whitney U test: $U=38.000$, $z=-1.415$, $N_{naive}=13$, $N_{experienced}=9$, $p=0.186$]. The
 738 same results were obtained when examining only the choices of adults [$M_{naive}=0.679$,
 739 $M_{experienced}=0.536$, Mann-Whitney U test: $U=13.500$, $z=-1.456$, $N_{naive}=7$, $N_{experienced}=7$, $p=0.165$].

740 These findings suggest that experience in earlier experiments is not responsible for the consistent
741 preference for hinderers that we found across our studies.

742 *Within-Session Analysis*

743 To determine whether bonobos learned or shifted their preference within the session, we
744 compared choices in the first half of the session with those in the second half and found no
745 difference test [Wilcoxon signed rank test, $z = -0.120$, $N = 22$, $T+ = 6$, ties = 10, $p = 0.904$].

746

747 **Experiment 3**

748 *Order Effects*

749 We also investigated order effects in Experiment 3, although power for this analysis was
750 even more limited. We compared Experiment 3 shift in choice for the hinderer between subjects
751 who had participated in Experiment 1 or 2 ($N=13$ experienced individuals) and those who had
752 participated in neither ($N=5$ naïve individuals). Again, naïve subjects showed a slight stronger
753 effect ($M=0.15$ shift toward hinderer between baseline and test) than experienced individuals
754 ($M=0.125$), and a Mann-Whitney U test revealed no difference between groups [$U=30.000$, $z=-$
755 0.258 , $p=0.849$].

756 *Within-Session Analysis*

757 To determine whether bonobos learned or shifted their preference within the test phase of
758 the session, we compared choices in the first half of the test phase with those in the second half
759 and found no difference [Wilcoxon signed rank test, $z = -0.243$, $N = 18$, $T+ = 8$, ties = 4, $p =$
760 0.808].

761

762 **Experiment 4**

763 *Developmental Analyses*

764 To investigate whether the developmental effect identified in Experiments 1 and 2
765 extends to our dominance paradigm, we again split the sample into adults and subadults and
766 repeated our analyses. Adults showed a preference for the dominant agent in the test condition
767 [$N=18$, $M=0.611\pm0.042$, $p=0.023$] but no preference for the respective agent in the control
768 [$N=18$, $M=0.542\pm0.030$, $p=0.180$]. In contrast, subadults showed no preference in either
769 condition [$N=6$, test $M=0.583\pm0.053$, $p=0.157$; control $M=0.500\pm0.000$, $p=1.000$]. Comparisons
770 between conditions revealed a marginally significant effect in adults but not subadults [related
771 samples Wilcoxon signed rank tests, adults: $N=18$, $p=0.096$; subadults: $N=6$, $p=0.157$]; however,
772 sample size was particularly small in subadults.

773

774

775 **DATA AND SOFTWARE AVAILABILITY**

776 Data are tabulated in the Supplementary Information (Tables S1-S4).

777

778 **MULTIMEDIA FILES**

779 **Movie S1. Experiment 1 animations, Related to Figure 1 and STAR Methods**

780 **Movie S2. Experiment 1 procedure, Related to Figure 1 and STAR Methods**

781 **Movie S3. Experiment 2 procedure, Related to Figure 3 and STAR Methods**

782 **Movie S4. Experiment 4 animations, Related to STAR Methods**

783 **Table S1. Subject characteristics and choices in Experiment 1, Related to Figures 1 and 2.**

784 **Table S2. Subject characteristics and choices in Experiment 2, Related to Figures 2 and 3.**

785 **Table S3. Subject characteristics and choices in Experiment 3, Related to Figures 2 and 3.**

786 **Table S4. Subject characteristics and choices in Experiment 4, Related to Figure 2.**