

Current Biology

Bonobos Prefer Individuals that Hinder Others over Those that Help

Highlights

- Bonobos discriminate between agents that either help or hinder others
- Whereas humans already prefer helpers by 3 months of age, bonobos favor hinderers
- Bonobos' preference may stem from attraction to dominant individuals
- This form of prosocial preference may be derived in humans

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In Brief

Krupenye and Hare investigate bonobos' preference for individuals that help versus hinder others. Whereas human infants already show a preference for helpers, bonobos favored hinderers. A preference for those that help others may be a derived trait in humans, providing a key building block at the foundation of humans' uniquely cooperative nature.



Bonobos Prefer Individuals that Hinder Others over Those that Help

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SUMMARY

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

RESULTS

The prosocial preference hypothesis suggests that bonobos exhibit their distinct pattern of cooperation in part because

they share a preference with humans for those who are prosocial toward others. Alternatively, the dominance hypothesis suggests that, although the outcome of bonobo cooperation is often human-like, bonobos, unlike humans, are more attracted to individuals that are antisocial in third-party interactions as these individuals are more likely to be dominant, powerful allies [25–28]. To test the prosocial preference and dominance hypotheses, we showed bonobos displays in which one actor behaved prosocially and another behaved antisocially toward a third party in one context. Then we allowed bonobos to choose between the actors in a completely unrelated context.

Experiment 1: Bonobos Prefer Animated Agents that Hinder Others

Twenty-four bonobos participated in experiment 1 (12 females, mean age (M_{age}) = 10.42 years, range = 4–19 years; Table 1; Table S1), completing both a test and a control condition on separate days, with condition order counterbalanced across subjects. In each condition, the experimenter sat at a table just outside the subject's enclosure, attracted them with food, and showed the subject two different animated videos on an iPad. The videos, modeled closely after the stimuli used by Hamlin et al. [6] to test human infants, depicted a pair of two-dimensional shapes interacting. As cues to their agency, each shape had two eyes with white sclera and dark pupils and exhibited goal-directed movements [29]. Eyes were chosen since experiments have shown that apes are sensitive to eye contact and direction [30], and bonobos are even more sensitive to eye gaze than are chimpanzees [31]. In the test condition, each video began with a circle, the climber, entering the scene and attempting but failing three times to climb a steep hill. On the third attempt, the climber encountered another agent. In the helper animation (Figure 1A; Movie S1), a second shape (i.e., the helper; e.g., a blue triangle) entered from below and pushed the climber up to the top of the hill before returning down the hill and exiting the screen. In the hinderer animation (Figure 1B; Movie S1), a different shape (i.e., the hinderer; e.g., a red square) entered from above and pushed the climber back down the hill before returning to the top of the hill and exiting the screen. Videos were of equal length, and the helper and hinderer each spent approximately the same amount of time on screen and in contact with the climber.

Following Hamlin et al. [6], we designed two control animations to examine the influence of the nonsocial features of our experimental animations. Each control animation was a variant



Table 1. Subject Characteristics and Participation in Experiments 1–4

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

For sex, “M” refers to males and “F” to females. Age refers to age estimate in years. Asterisks denote subjects tested by Herrmann et al. [26]. Exp., experiment.

of an experimental video in which an agent pushed an eyeless, inanimate circle up or down the hill (see [Figures 1C](#) and [1D](#)). Unlike the climber in the experimental animations, the inanimate circle in these control videos exhibited no independent movement or goal-directed action. Otherwise, the upward animation ([Movie S1](#)) mimicked the actions of the helper animation and the downward animation ([Movie S1](#)) mimicked those of the hinderer animation.

Test and control sessions each involved four trials in which subjects first witnessed the two animations for that condition in a loop (i.e., test: helper and hinderer animations; control: upward and downward animations) and then were allowed to choose between paper cutouts of the agents placed on top of small pieces of apple ([Movie S2](#)). Based on previous work with infants and nonhuman apes, we used reaching behavior as a measure of preference (e.g., [6, 32]). To avoid shaping subjects’ preferences, we used non-differential rewarding. Subjects received the same quality and quantity of food regardless of their choice. The helping and hindering behavior in the test events did not involve food. Therefore, a preference, for example for helpers, could not be based on subjects evaluating the agent as a social tool for food acquisition. Unless otherwise noted, all analyses for all experiments represent two-tailed one-sample Wilcoxon signed-rank tests of the proportion of trials in which subjects chose a particular agent.

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

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

Experiments 2 and 3: Bonobos Prefer Unfamiliar Human Actors that Hinder Others

The preferences that we observed for arbitrary shapes acting with agency may translate into the natural social interactions of

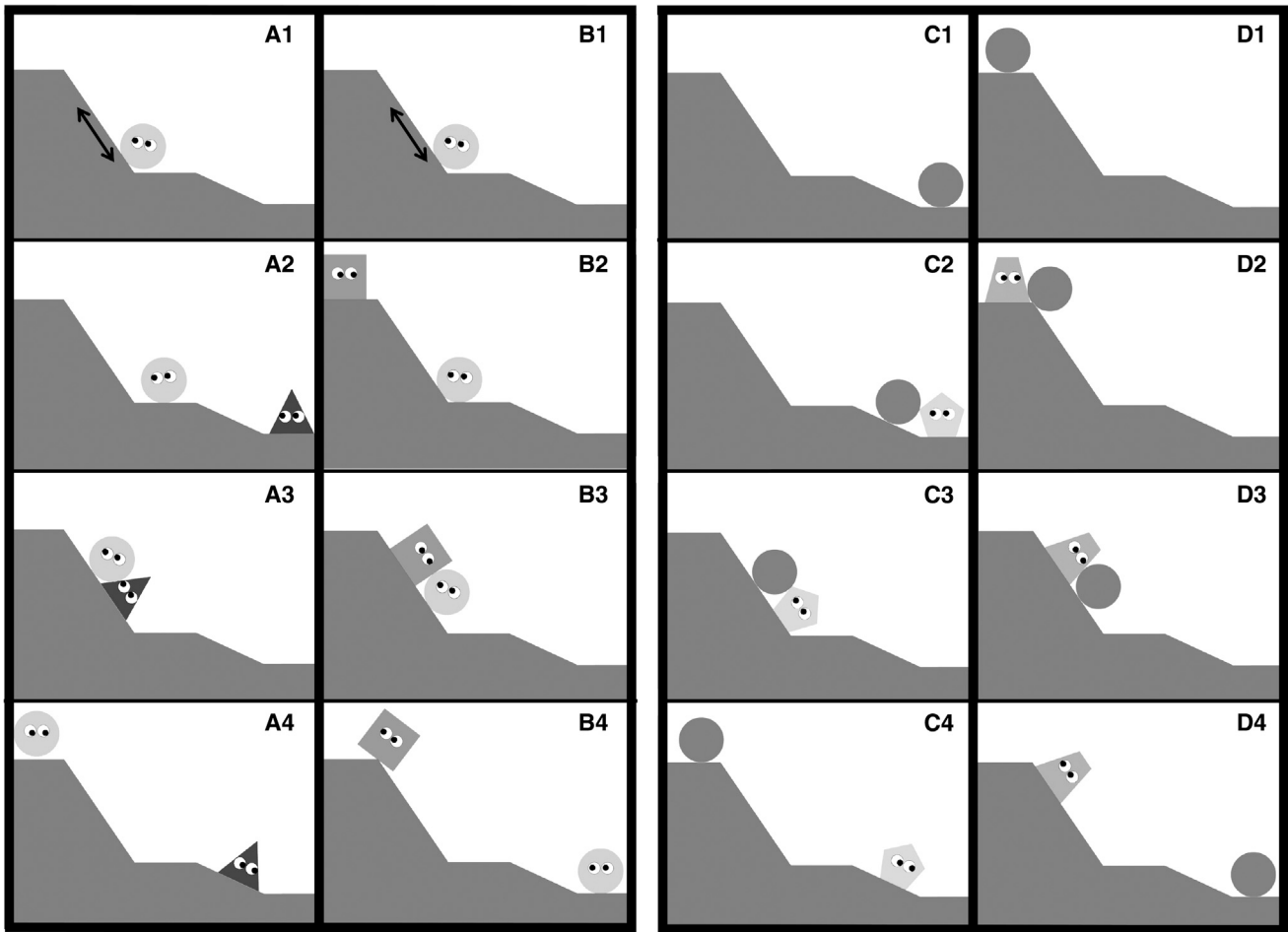


Figure 1. Frames from Experiment 1 Video Stimuli

Helper animation (A), hinderer animation (B), upward animation (C), and downward animation (D). In both the helper (A) and hinderer (B) animations, the climber (circle) tries but fails to scale the hill (A1 and B1) three times before encountering another agent. In the helper animation, the helper (here, a triangle) enters from below (A2), pushes the climber up the hill (A3), and exits the screen (A4). In the hinderer animation, the hinderer (here, a square) enters from above (B2), pushes the climber down the hill (B3), and exits the screen (B4). The upward animation (C) begins with a static ball at the base of the hill (C1). The upward agent enters from below (C2), pushes the ball up the hill (C3), and exits the screen (C4). Conversely, the downward animation (D) begins with a static ball at the top of the hill (D1). The downward agent enters from above (D2), pushes the ball down the hill (D3), and exits the screen (D4). See also [Movies S1](#) and [S2](#) and [Table S1](#).

bonobos. However, in a previous experiment, bonobos did not discriminate between human experimenters that they observed either attempting to share food with or steal food from another experimenter [26]. Therefore, in experiment 2, we tested whether the hinderer preference from experiment 1 was robust enough to generalize to a real-world social interaction involving object-centered prosocial and antisocial behavior by unfamiliar human actors.

Twenty-two bonobos (11 females, $M_{\text{age}} = 10.63$ years, range = 4–17 years; [Table 1](#); [Table S2](#)) participated in experiment 2. Experiment 2 consisted of eight trials, each involving a demonstration phase and a choice phase ([Figure 3](#); [Movie S3](#)) modeled after a similar social preference task [26]. In the demonstration phase, subjects watched as a neutral actor dropped a toy out of reach, a helper retrieved the toy and attempted to return it to the neutral actor, and a hinderer prevented the transfer by aggressively snatching the toy. In the choice phase, which followed immediately, the helper and hinderer approached the bo-

nobo simultaneously with a piece of apple in their hands. Subjects received food from whichever actor they approached first.

Overall, subjects tended to select the hinderer more frequently than the helper ($M = 0.551 \pm 0.036$ of trials), but not significantly above chance ($n = 22$, $p = 0.158$; [Figure 2B](#)). Since in experiment 1 only adults exhibited a hinderer preference, we again separated our sample into adults and subadults, replicating the age-dependent pattern. Adults, but not subadults, exhibited a significant preference for the hinderer (adults: $n_{\text{aged}9-17} = 14$, $M = 0.607 \pm 0.047$, $p = 0.047$; subadults: $n_{\text{aged}4-8} = 8$, $M = 0.453 \pm 0.040$, $p = 0.257$; [Figure 2B](#)), extending the experiment 1 finding to a completely different real-world context.

In experiment 3, we further tested the robustness of adult bonobos' preference for hinderers by replicating experiment 2 but including an additional baseline phase to assess and control for subjects' arbitrary preferences for the experimenters. Experiment 3, therefore, tested whether bonobos would shift their initial

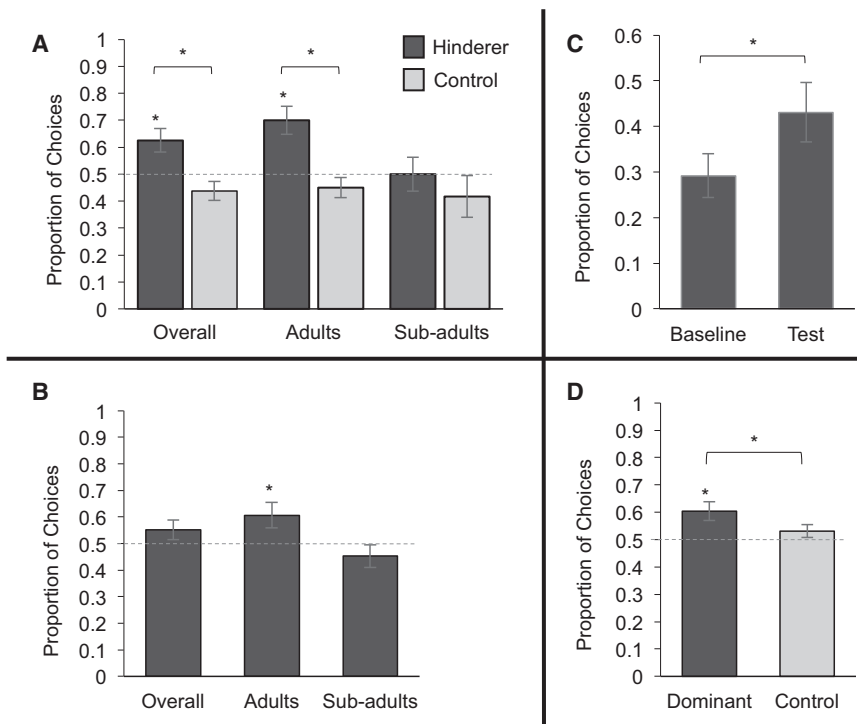


Figure 2. Results of Experiments 1–4

(A) Mean proportion of choices for the hinderer and control in experiment 1, overall and for adults and subadults.

(B) Mean proportion of choices for the hinderer in experiment 2, overall and for adults and subadults.

(C) Shift in proportion of choices for the hinderer between baseline and test in experiment 3.

(D) Mean proportion of choices for the dominant and control in experiment 4.

Asterisks indicate significant effects ($p < 0.05$). Error bars depict the SE. See also Tables S1–S4.

preference toward the hinderer once he began to behave antisocially.

Experiment 3 employed identical methods to experiment 2 (Figure 3), except that subjects participated in four baseline trials before completing four test trials ($n = 18$ adult bonobos, $M_{\text{age}} = 12.33$ years, range = 10–18 years nine females; Table 1; Table S3) (see [33] for a similar design). Baseline trials only involved the choice phase of the procedure from experiment 2, whereas test trials included the demonstration and choice phases. Additionally, after making their choice, subjects did not receive food from either experimenter. If subjects approached one experimenter during the majority of baseline trials, this experimenter was assigned the role of helper. If subjects approached the experimenters equally during baseline trials, roles were assigned semi-randomly, with the aim of counterbalancing the role played by each experimenter across subjects [33].

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

Experiment 4: Bonobos Prefer Animated Agents that Are Dominant

In experiment 4, we further tested the dominance hypothesis—that subjects' hinderer preference might be explained by an attraction to individuals perceived as dominant, since dominant individuals may be the most desirable allies or social partners. Although in principle prosocial and antisocial individuals can

be dominant or subordinate, antisocial behavior is often used to establish and maintain dominance, and the specific antisocial behaviors exhibited by hinderers in our studies and those with human infants resemble dominance interactions: the hinderer prevails over the neutral agent or the helper in reaching his goal (of descending the hill or acquiring the toy) [34–36]. Therefore, according to the dominance hypothesis, we predicted that bonobos would exhibit a preference for an antisocial dominant over a subordinate as they did for hinderers over helpers.

Experiment 4 was identical to experiment 1, except for the animations ($n = 24$, $M_{\text{age}} = 10.83$ years, range = 4–17 years, ten females; Table 1; Table S4). In the test session (Movie S4), subjects watched a video in which two animated agents competed for access to a central location in the scene, with the dominant agent repeatedly displacing the subordinate one, a dominance interaction familiar to nonhuman primates (see also seminal work with humans by Heider and Simmel [37]). To ensure that a preference in the test session did not stem from perceptual features, in the control session (Movie S4) subjects witnessed the same video (with new agents) except that the agents' actions were separated in time such that they were no longer contingent and therefore the agents should not be perceived as being dominant or subordinate to one another. As in experiment 1, all subjects participated in both conditions on separate days, with condition order counterbalanced across individuals.

Subjects exhibited a significant preference for the dominant agent ($n = 24$, $M = 0.604 \pm 0.033$, $p = 0.008$; Figure 2D). No subjects chose the subordinate on a majority of trials, whereas eight favored the dominant. In the control, bonobos showed no preference for either agent ($n = 24$, $M = 0.531 \pm 0.023$, $p = 0.180$; Figure 2D). One favored the subordinate control and four the dominant control. Within-subject comparisons revealed that subjects selected the dominant agent significantly more than its control counterpart (related-samples Wilcoxon signed-rank test, $n = 24$, $p = 0.035$; Figure 2D). When the sample was split into adults and subadults, the effects replicated only in adults, although the subadult sample size was notably smaller ($n = 6$; see STAR Methods). Given that bonobos' dominance preference is driven by eight subjects, it's possible that this

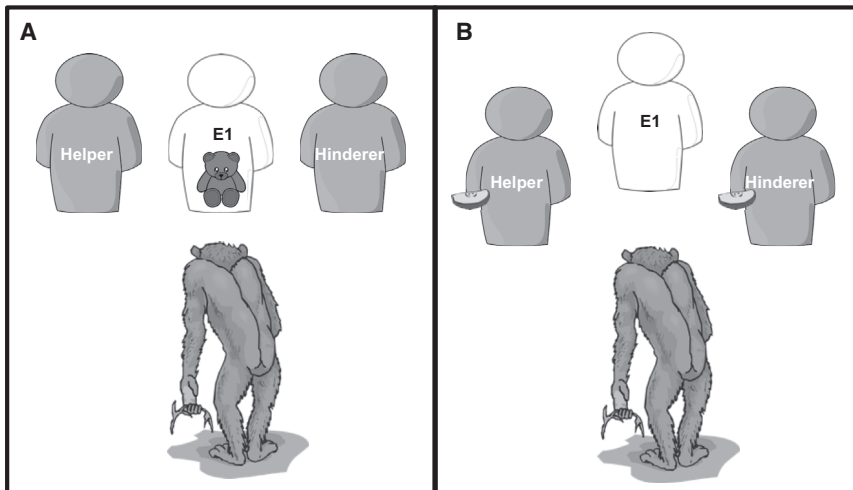


Figure 3. Experimental Procedure of Experiments 2 and 3

(A) Demonstration phase. 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](#).

effect explains some, but not all, of the preference for hinderers documented in the first three experiments.

DISCUSSION

Our results support the predictions of the dominance hypothesis and raise the possibility that the motivation to prefer prosocial individuals evolved in humans after their divergence from the other apes. In three experiments, adult bonobos spontaneously chose a human or animated agent that hindered another individual over one that helped. In contrast, by 3 months of age, human infants already show the *opposite* preference in related paradigms [6–8]. Bonobos failed to show a human-like preference despite their relative tolerance and prosociality in dyadic interactions [11, 15]. However, bonobos were sensitive to the actors' goal-directed actions toward others, clearly discriminating between helpers and hinderers, even when they were just animated shapes with eyes. This finding suggests that bonobos do track interactions between third parties and evaluate potential social partners based on these interactions [38, 39].

Our main finding is reproducible, having been replicated in three different experiments involving multiple paradigms with both humans and animated agents as actors. Our experiments controlled for attraction to different colors, shapes, or motion patterns. Agent color and shape were counterbalanced between subjects and, when key social features were removed, bonobos showed no preference for control agents that exhibited similar motion patterns. The fact that bonobos showed consistent preferences across all of our studies also provides validation for the more artificial but completely novel animation-based experiments. Because we used non-differential or zero rewarding and few trials, subjects did not have an opportunity to form preferences based on food acquisition. Moreover, our use of both novel animated agents and unfamiliar human experimenters allowed us to eliminate biases in social preference based on social information that is unrelated to the goals of our study (such as sex, age, reproductive status, and size of the agents). Critically, bonobos' preferences were tested in a context that differed from the one in which the actors' prosocial and antisocial behavior was demonstrated, minimizing the possibility that, at

the moment of choice, subjects were simply expecting to be able to use the actor as a context-specific social tool. Although the results of experiment 1 could be interpreted as bonobos preferring to steal food from the hinderer (since food accompanied their choices), experiments 2–4 suggest that this was not the case. For one, this interpretation would suggest that, in experiment 4, bonobos also preferred to steal from a dominant, which is antithetical to the concept of dominance and thus unlikely. Moreover, experiments 2 and 3 were based on a paradigm in which bonobos preferred to approach an individual who had recently groomed or played with them over one who had not [33], suggesting that these measures reflect social affinity rather than acts of punishment. Finally, the interpretation that bonobos prefer dominant hinderers accords with natural observations in which bonobos exhibit courtesy begging toward high-ranking individuals to build and test relationships [16].

Bonobos may prefer hinderers because they appear to be more dominant than helpers. When intervening in third-party conflicts, primates often support the higher-ranking contestant or the one who is already winning (i.e., “winner support”), and they may gain reproductive benefits from doing so [24, 40]. For example, high-ranking male chimpanzees, who often prevent others from mating, have been shown to be more tolerant of mating by their supporters [41]. In food sharing contexts, wild bonobos preferentially beg for food from dominants even when they can easily obtain the same food themselves, perhaps to test their social tolerance [16]. Recent evidence also suggests that female bonobos may exert especially high levels of choice in mating decisions, selecting the highest-ranking males [42]. In support of this dominance preference interpretation, in experiment 4, bonobos favored a dominant agent over a subordinate one. Hindering and dominance are not inextricably linked, however, and, as such, research with humans and nonhuman animals should continue to investigate understanding of these qualities and the relationship between preferences for prosocial versus antisocial agents and for dominants versus subordinates.

Future work should also examine whether there are contexts in which bonobos do prefer prosocial individuals (e.g., in response to conspecifics). Our spontaneous measures can also be extended to a range of species. Capuchin monkeys (*Cebus apella*) would be a good prospect since in some contexts they show a preference for helpers over non-helpers. However, they have yet to be tested for their preference between helpers and hinderers [43]. Our work will also need to be extended to other

apes to provide more resolution on the phylogenetic history of this trait in our lineage. For example, chimpanzees and orangutans spontaneously requested food from a human they had observed sharing food with a third party over one who had refused to share [26–28]. However, it is unclear whether this potential prosocial preference would generalize to cases, like those investigated in our experiments and experiments with human infants, where participants must evaluate others based on prosocial and antisocial interactions that are not immediately relevant to the participants. Chimpanzees prefer to seek food from an individual who has shared food moments before, but would they also prefer to interact with an individual who has previously helped a third party to access a goal object, as human infants do, or would they instead prefer to interact with someone who has previously thwarted a third party's goal, like bonobos? Further work on chimpanzees' social preferences and evaluative cognition is necessary to clarify whether bonobos or humans show the more derived preference.

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

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information includes four tables and four movies and can be found with this article online at <https://doi.org/10.1016/j.cub.2017.11.061>.

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AUTHOR CONTRIBUTIONS

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

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Tables S1–S4	N/A	N/A
Experimental Models: Organisms/Strains		
<i>Pan paniscus</i>	Lola ya Bonobo Sanctuary, Kinshasa, Democratic Republic of Congo	N/A
Software and Algorithms		
SPSS Version 23	IBM	N/A

CONTACT FOR REAGENT AND RESOURCE SHARING

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

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Forty-three semi-free-ranging bonobos (aged 4–19; 21 females; see [Table 1](#)) were tested at Lola ya Bonobo sanctuary in Kinshasa, Democratic Republic of Congo (<http://www.lolayabonobo.org>) during two field seasons (October–December, 2012: experiment 1; May–June, 2015: experiments 2–4; see [Table 1](#)). Animal husbandry and care practices complied with the Pan-African Sanctuary Alliance (PASA) Primate Veterinary Healthcare Manual, as well as the policies of Lola ya Bonobo Sanctuary. These non-invasive behavioral studies were approved by Duke University IACUC (A035-14-02) and adhered to host country laws. Apes in African sanctuaries are typically born in the wild, and enter the sanctuary after being confiscated at an early age (~2–3 years old) as a result of the trade in wildlife for pets and bushmeat. Previous work indicates that sanctuary apes are psychologically healthy relative to other captive populations [44]. All subjects were socially housed, and free-ranged in large tracts of tropical forest during the day (5–40 hectares across groups). In the evening, all apes spent the night in indoor dormitories (12 m²–160 m²). Apes were tested individually in these familiar dormitory buildings. Following testing, all subjects were released back with their larger social groups outside. Subjects had *ad libitum* access to water and were not food-restricted during testing. In addition to food naturally available in their forest enclosures, apes were fed a variety of fruits, vegetables, and other species-appropriate foods two to four times daily. Apes were tested on only one session per day and all tests were voluntary. If apes refused to approach the experimenters and participate in the studies or if they became upset (e.g., screaming, banging), they were released from the testing room. In experiments 1 and 4, if a subject did not make a choice within 5 min, the session was aborted and the subject excluded from analyses (one subject in experiment 4). In experiments 2 and 3, if a subject did not make a choice within 1 min, the trial was repeated. If the subject did not make a choice for more than three trials, the session was aborted and the subject was excluded from any analyses (two subjects in experiment 2 and eight in experiment 3). In addition, one subject, who was small enough to reach his entire arm through the bars (instead of just his fingers), was excluded from experiment 1 for repeatedly disrupting the experimenter's attempts to present the choices and ultimately making it impossible for the experimenter to test him. One subject was excluded from experiment 2 due to experimenter error (i.e., failing to correctly counterbalance experimenter locations across trials).

METHOD DETAILS

Experiment 1

Procedure

Subjects were tested alone in a testing room. The experimenter positioned himself at a small table just outside of the testing room, across the mesh from the subject. The experimenter presented video stimuli to the subjects via an iPad and then allowed subjects to choose between paper cutouts of animated agents from the videos ([Movies S1](#) and [S2](#)). Importantly, previous work has demonstrated that apes can treat animated agents as goal-directed [29], track the goals and third-party interactions of agents on screens [45–47], have some understanding of iconic representation [48, 49], equate 2-D depictions in video with real life objects [50], and treat images of familiar individuals on a monitor as representative of those individuals [51, 52].

In both test and control sessions (which occurred on separate days, with order counterbalanced between subjects), subjects were first familiarized to the relevant animations on the iPad (i.e., test session: helper and hinderer animations; control session: upward and

downward animations) as they alternated in a loop for a total of four presentations of each animation. To begin presentation of the animations, the experimenter attracted the subject's attention by calling her name and began the video sequence, shifting the direction of the iPad to maximize viewing in cases where the subject moved or shifted her gaze. Additionally, subjects who moved to the back of the room (i.e., away from the iPad) or looked away from the iPad for more than several seconds were offered small pieces of food to regain their attention.

Four test trials were conducted immediately following familiarization. Before being given a choice in each test trial, subjects again watched both animations once (order counterbalanced within-subjects). After the experimenter finished showing the animations, he either moved the table so that the subject was sitting at the midline of the table or used a piece of food to attract the subject to that central location. This process ensured that during the choice phase, subjects had equal access to both options. The experimenter then simultaneously placed two pieces of apple on the middle of the table, held up 5cm² cutouts of the two agents (i.e., test session: helper and hinderer; control session: upward and downward agents) above the pieces of apple for 2 s, laid them on top of the pieces of apples, moved the agents (and now occluded apples) to opposite sides of the table, pushed the sliding table-top forward to allow the subject to make a choice, and started a stop watch. To make a choice, subjects gestured toward one of the agents (i.e., protruding her finger through the mesh to touch the agent). Once the subject had made a choice, she was provided the paper cutout and associated apple. The other agent and apple piece were removed from the table. If a subject double-pointed (i.e., used both hands to select both options at the same time) or did not make a choice within a minute, the experimenter pulled the table back, and waited a few seconds before presenting the choice again. To avoid influencing the subject's choice, all actions involved in presenting the choices occurred simultaneously, the locations of the helper and hinderer replicas (or upward and downward controls) were counterbalanced across trials, and the experimenter looked directly at the subject while pushing the table forward and waiting for the subject to make a choice [32].

Design

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

To control for the fact that the helper and upward agent enter from the opposite side of the scene as the hinderer and downward agent, we created mirrored versions of all videos. For each subject, half of the presentations of each video were the original version and half were the mirrored version. We counterbalanced the order of original versus mirrored presentations within and between subjects and we counterbalanced which occurred on the first trial between subjects.

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

Scoring

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

Experiment 2

Subjects participated in a series of eight trials in a single session. Each trial consisted of a demonstration phase followed by a choice phase (Movie S3). In the demonstration phase, a pair of experimenters sat on either side of a third neutral actor (E1) just outside the subject's enclosure. These experimenters (the helper and hinderer) were two Congolese men of similar age who were familiar with the sanctuary but had never interacted with the bonobos. Their roles were counterbalanced across subjects. E1 was playing with a plush toy, tossing it in the air and mimicking bonobo laughter, when he dropped the toy out of reach and then grasped for it effortfully—vocalizing and gazing at it with arm outstretched. The helper calmly picked up the toy, made eye contact with E1, and attempted to return the toy to E1. Before E1 could take the toy, the hinderer snatched the toy from the helper, aggressively grunted, and turned his back to the other two, surreptitiously depositing the toy in a bucket between himself and E1. As a familiarization, subjects first watched the demonstration two times (and then a third time as part of the first trial) to ensure that by the first choice phase they were familiar with the behavior of each experimenter. E1 then said, "ok," and the three stood up with their backs to the subject, beginning the choice phase. E1 gave the helper and hinderer a piece of apple, made sure the experimenters were roughly 1 m apart, positioned the bonobo centrally with an additional piece of food, and then directed the experimenters to simultaneously turn toward the bonobo and approach her with the food in their outstretched hands. When the experimenters arrived, E1 started a stopwatch and the bonobo had 1 min to choose between the experimenters. A choice was made if the subject approached one experimenter and

gestured toward the food with her hand or mouth (i.e., put her hand or mouth up to the mesh where the experimenter held the food). She was then given the piece of apple by the experimenter she chose. All experimenters then turned around and the unchosen experimenter's food was placed in the bucket. The experimenters sat in the appropriate location for the next trial's demonstration phase, which began immediately.

Design

The roles of the experimenters remained constant for a given bonobo, but were counterbalanced across subjects. We counterbalanced the locations of the helper and hinderer across trials (i.e., which experimenter was positioned to the left and which to the right of E1). Half of the subjects experienced ABBABAAB order while the other half experienced BAABABBA order. Experimenters remained in the same location for the demonstration and choice phases of a given trial. During the two familiarization demonstrations that preceded the first trial, experimenters occupied the positions assigned to them for the first trial.

Scoring

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

Experiment 3

Procedure and Design

The procedure and design of this study were identical to that of experiment 2, except for three key differences. First, we altered the choice phase of the task. Although the helper and hinderer still held out a piece of apple to the bonobo, this food was not given to the subject after she made her choice. That is, the helper and hinderer never provisioned the subject; the subject only received food from E1, the neutral actor. Second, test trials were preceded by four baseline trials to measure any pre-existing preferences for the experimenters. Baseline trials involved only the choice phase from experiment 2. If the subject demonstrated a preference for one experimenter during baseline trials (i.e., choosing him three or four times), that experimenter was assigned to the role of the helper and the less-preferred experimenter was assigned the role of hinderer. If the subject chose each experimenter twice, the experimenters were assigned to their roles pseudo-randomly, based on the goal of counterbalancing each experimenter's roles across subjects. Finally, subjects only participated in four instead of eight test trials (following the four baseline trials). As in experiment 2, subjects witnessed the demonstration three times before the choice phase of the first test trial, and one additional time before the choice phase of each of the other test trials. Locations of the experimenters were counterbalanced across trials, with the same order repeated in both baseline and test trials for a given subject. Half of subjects experienced ABBA order and the other half BAAB order.

Scoring

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

Experiment 4

Procedure and Design

The procedure and design of experiment 4 were identical to those of experiment 1, save for the use of different animations. In addition, rather than witnessing two separate animations, showcasing the behavior of each agent (e.g., like the helper and hinderer animations), in experiment 4, each condition featured a single animation depicting interactions between the two agents. The test animation featured a dominant agent and a subordinate agent engaging in a dominance contest ([Movie S4](#)). In the animation, the subordinate moved to a contested location and was displaced several times by the dominant agent. That is, each time that the subordinate moved to the contested location, the dominant appeared quickly, pushed the subordinate off of the spot, and returned to occupy the location briefly. Eventually the dominant moved from the contested location. Once the dominant arrived at its rest location, the subordinate then slowly inched back to the contested location before being displaced again by the dominant.

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

Scoring

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

QUANTIFICATION AND STATISTICAL ANALYSIS

Proportions of choices for the hinderer (experiments 1-3), downward agent [i.e., hinderer control] (experiment 1), dominant (experiment 4), and dominant control (experiment 4) were calculated for each subject. Analyses of bonobos' preferences within and between conditions (two-tailed one sample and related samples Wilcoxon signed rank tests) and calculation of reliability on coding (Cohen's Kappa) were performed using SPSS, version 23.

To test whether humans are precocious relative to our closest relatives in the development of third-party social evaluation, we examined the relationship between age and social preference in bonobos. We split our subjects into adults and subadults, using a relatively conservative measure of maturity. Although in the wild bonobo females disperse from their natal group by ten years of age, individuals at Lola ya Bonobo sanctuary begin to reach sexual maturity at the very earliest at age 8 [15, 53]. Therefore, for developmental analyses, we grouped individuals 9 and above into our adult cohort and those 8 and below into our subadult cohort.

Experiment 1

Unintentional Cueing Check

As an additional precaution to ensure that subjects' choices were not influenced by unintentional cueing in the experimenter's presentation of the choices in the test phase, two additional coders blind to condition and the role of each agent reviewed the videos to determine if during the presentation of choices in either experiment the experimenter had placed either choice closer to the edge of the table, or stopped moving one choice earlier than the other. VirtualDub was used to allow coders to view the experimental videos frame by frame (30 frames/second). For each trial, coders skipped to a time when both options had been presented but before the subject had made a choice. To test whether E subconsciously placed the agents in a manner that might encourage the choice of one agent over the other simply because it was slightly closer to the subject, coders recorded whether one agent was placed closer to the edge of the table than the other. Visibility in videos permitted this "moved closer" coding in 190 of 192 trials. To test whether E subconsciously placed the agents in a manner that might encourage the choice of one agent over the other simply because the movements of the two agents ended at slightly different times, coders watched frame by frame in reverse, recording the frame for the moment when each hand first moved the agent. Watched forward this is the hand's final movement of the agent to its final choice location. One agent was considered to have stopped moving perceptibly earlier than the other if the difference between the left and right hands' final movement times was greater than 6 frames (200 ms) since this is the minimum time differential nonhuman apes need to perceive events [54]. Visibility in videos permitted this "moved later" coding in 182 of 192 trials. Reliability on these measures was substantial [55] [moved closer: 91.1% agreement, Cohen's kappa = 0.767; moved later: 95.6% agreement, Cohen's kappa = 0.754].

To determine if unconscious movement measures contributed to our results, we reanalyzed the data from experiment 1, excluding the trials on which both coders agreed that one agent was moved closer (35 trials) or moved later (14 trials). In both cases, we replicated our findings in the test condition: subjects exhibited a significant preference for the hinderer [one sample Wilcoxon signed rank tests: moved closer trials excluded: $n = 23$, $p = 0.013$; moved later trials excluded: $n = 24$, $p = 0.015$]. Reanalysis of the control condition revealed that with moved closer trials excluded subjects had a preference for the upward bound agent [$n = 24$, $p = 0.043$], the agent whose motor patterns mirrored the helper, not the hinderer, and with moved later trials excluded subjects had no preference for either agent [$n = 24$, $p = 0.114$]. We also replicated our finding that subjects' choices in the test condition were significantly different from their patterns of choice in the control [related samples Wilcoxon signed rank tests: moved closer trials excluded: $z = -2.833$, $n = 23$, $T+ = 3$, ties = 4, $p = 0.005$; moved later trials excluded: $z = -2.913$, $n = 24$, $T+ = 3$, ties = 8, $p = 0.004$]. These results suggest that subjects' selection of the hinderer in the test condition cannot be accounted for by a preference for the agent's motor pattern, and that presentation of one agent closer or later than the other is unlikely to have influenced our findings.

Developmental Analyses

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

Within-Session Analyses

To assess how quickly bonobos formed their preferences we examined their choices on the first trial. Subjects did not show a first trial preference for either agent in the test [Binomial test, $n = 24$, $p = 1.000$] or control [Binomial Test, $n = 24$, $p = 0.064$], and showed no difference between conditions [Wilcoxon signed rank test, $z = -1.508$, $n = 24$, $T+ = 8$, ties = 13, $p = 0.132$]. For each condition, we then compared subjects' preferences in the first half of the session with that of the second half. There were no differences in choice patterns between the first and second half of the test [Wilcoxon signed rank test, $z = -0.443$, $n = 24$, $T+ = 6$, ties = 11, $p = 0.658$] or control

conditions [Wilcoxon signed rank test, $z = -0.707$, $n = 24$, $T_+ = 2$, ties = 19, $p = 0.480$], indicating that subjects' choices (i.e., preference for the hinderer and no preference among upward/downward agents) were consistent throughout each session.

Experiment 2

Order Effects

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

Within-Session Analysis

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

Experiment 3

Order Effects

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

Within-Session Analysis

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

Experiment 4

Developmental Analyses

To investigate whether the developmental effect identified in experiments 1 and 2 extends to our dominance paradigm, we again split the sample into adults and subadults and repeated our analyses. Adults showed a preference for the dominant agent in the test condition [$n = 18$, $M = 0.611 \pm 0.042$, $p = 0.023$] but no preference for the respective agent in the control [$n = 18$, $M = 0.542 \pm 0.030$, $p = 0.180$]. In contrast, subadults showed no preference in either condition [$n = 6$, test $M = 0.583 \pm 0.053$, $p = 0.157$; control $M = 0.500 \pm 0.000$, $p = 1.000$]. Comparisons between conditions revealed a marginally significant effect in adults but not subadults [related samples Wilcoxon signed rank tests, adults: $n = 18$, $p = 0.096$; subadults: $n = 6$, $p = 0.157$]; however, sample size was particularly small in subadults.

DATA AND SOFTWARE AVAILABILITY

Data are tabulated in the [Supplemental Information \(Tables S1–S4\)](#).