Chimpanzees play the ultimatum game

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Is the sense of fairness uniquely human? Human reactions to reward division are often studied by means of the ultimatum game, in which both partners need to agree on a distribution for both to receive rewards. Humans typically offer generous portions of the reward to their partner, a tendency our close primate relatives have thus far failed to show in experiments. Here we tested chimpanzees (Pan troglodytes) and human children on a modified ultimatum game. One individual chose between two tokens that, with their partner’s cooperation, could be exchanged for rewards. One token offered equal rewards to both players, whereas the other token favored the chooser. Both apes and children responded like humans typically do. If their partner’s cooperation was required, they split the rewards equally. However, with passive partners—a situation akin to the so-called dictator game—they preferred the selfish option. Thus, humans and chimpanzees show similar preferences regarding reward division, suggesting a long evolutionary history to the human sense of fairness.

Humans often make decisions that seem irrational from an economic perspective. For instance, they may engage in behavior that actually decreases their absolute wealth. One explanation for these decisions is that humans are not only concerned with their own rewards but also the rewards of others (1). Human reactions to reward distributions have been extensively studied by means of experimental economics tasks, in particular the ultimatum game (2–5) and the dictator game (6, 7). In the ultimatum game (UG), one individual (the proposer) is asked to split a quantity of money with another individual (the respondent). If the respondent accepts the offer, both players are rewarded using the proposed split. If the respondent rejects the offer, then neither player is rewarded (2). The dictator game (DG) is a variant of the UG in which the respondent has no chance to reject the offer and thus all of the proposer’s offers are “accepted.”

Proposers in both the UG and DG generally go against their own short-term interests in offering the partner more than the minimum possible amount of money (8). In UGs, people from Western cultures typically offer around 50% of the available money (3–5), even in anonymous one-shot games that lack any future interaction. In DGs, people still offer more of the money than a purely self-interested model would suggest, but offers are lower than in UGs (4, 6, 7). The reasons why humans typically offer more than self-interested models would predict are twofold. First, humans may be concerned with the welfare of others and thus behave more generously out of an altruistic motivation (1, 4). Second, they may anticipate refusals of inequitable reward distributions during UGs and make larger offers to ensure that they are accepted, thus serving their own self-interest (4, 6, 7). Whereas either of these reasons is sufficient to drive human behavior in these tasks, they may also work in concert.

However, cultural norms of fairness vary across study populations (8). For example, the Lamelara of Indonesia typically offer more than a fair share (mean 58%), presumably because they are culturally dependent on large-scale cooperation (to hunt whales) and thus have mechanisms in place to share surplus resources. In contrast, the Hadza of Tanzania, who are hunter-gatherers who share food with group members because of cultural expectations and the fear of ostracism, make the lowest offers of any study population, and these offers are often rejected (9, 10). This likely occurs because of the specific experimental setting of the UG, which may reduce the fear of being ostracized, allowing the Hadza participants to follow their self-interest. In all cases, a given culture’s degree of cooperation, sharing, and punishment influences offers in economic games (8, 11). What remains unclear is how other primates, including one of our closest living relatives, the chimpanzee (Pan troglodytes), respond to these types of situations. Studying other primates may shed light on the evolutionary basis for the human tendency toward “fair” distributions.

As recent work has shown, nonhuman primates, particularly chimpanzees and capuchin monkeys (Cebus spp.), resemble humans in their decisions about cooperation (12–15) and their aversion to inequitable reward divisions (16–18). However, it is unclear how these same nonhuman primates respond to situations in which a peer can influence the outcome of a task, such as in the UG. In contrast to the human tendency to split rewards roughly equally (at least in most cultures), two previous studies found apes to be entirely self-interested: Proposers offered the smallest possible amount and respondents accepted virtually all offers (19, 20).

In these experiments, a food-delivery apparatus was set up so that the proposer could select between two divisions of the food rewards yet needed help from the respondent to access the food. Respondents either accepted offers by pulling the food within reach or refused offers by not acting for 30 s. This methodology differed from typical human UGs in substantial ways, however. First, the task used a complex mechanical apparatus, something not found in human UGs. Thus, direct comparisons to the human literature are challenging, as it is unclear that apes understand such technology. In other contexts, test designs avoiding technology have yielded dramatically different results (21, 22). Second, apes were tested repeatedly with members of their own social group, whereas humans are typically tested in one-shot games with anonymous strangers who are often not even in the same room (e.g., proposers and respondents never meet). It is unclear what effect, if any, an existing social relationship, social cues, and repeated interactions have on the dynamics of the game.

Third, apes were tested with food items, which are immediate reinforcers, whereas humans are typically tested with money, which lacks immediate value (e.g., cannot be consumed and must be traded for something of value). Chimpanzees seem to have strong prepotent responses to the visual presence of food, which may predispose them to accept offers regardless of reward distribution (23). In fact, respondents in both previous studies frequently accepted offers of zero, which they should not have done had they fully understood the task (24, 25). Finally, to refuse an offer, apes had to inhibit action for 30 s (i.e., not pull the food-delivery mechanism), whereas human refusals are active (i.e., they express their refusal). This difference may seem minor, but...
when humans were asked to wait 1 min to refuse an offer in a face-to-face, repeated-trials UG, they behaved like the apes and accepted most offers (26). Due to these differences in UG methodology in tests with humans and apes, it remains unclear to what degree decision-making similarities and/or differences reflect psychological or cognitive differences, as opposed to procedural differences. All that we can ever measure are choices; the challenge is to establish whether these choices represent preferences for certain outcomes.

There are sound evolutionary reasons to expect chimpanzees to be sensitive to unequal outcomes. They routinely cooperate by defending territory, form coalitions, hunt in groups, share food (27–29), and engage in reciprocal exchanges that suggest mental scorekeeping (refs. 30–32, although see ref. 33). For example, chimpanzees are sensitive to unequal outcomes in experiments, refusing to participate when a partner earns a better reward for equal effort, and occasionally even refusing a better reward when a partner receives less (16, 34). The ability to recognize and be sensitive to unequal outcomes would theoretically help them establish beneficial partnerships (34). Additionally, chimpanzees pay attention to intent, reacting more negatively to a partner deliberately stealing their food rather than one giving their food to another (35, 36). They also show “targeted helping,” which requires recognition of another’s needs and goals (37, 38).

There are anecdotal reports of chimpanzees equitably dividing rewards during nonexperimental encounters. In one example, an adolescent female broke up a fight between two juveniles over a leafy branch. The female broke the branch in two and then handed half to each juvenile without taking any for herself (39). Goodall (40) reported an interaction between two males, one of whom was in possession of meat. After repeated begging, the male without the meat threw a “violent tantrum.” Following this, the meat possessor ripped the prey in half and gave a portion to the second male. Based on these and similar observations as well as the overall levels of cooperation, sharing, and punishment observed among chimpanzees, we would expect them to make equitable offers in UGs.

The purpose of the present study was to investigate how sensitive chimpanzees are to reward distribution when their partner can affect it. If they are sensitive to partner effects, their choices in the UG should resemble those of humans. Proposers were presented with a choice of two tokens—a method that requires no apparatus and appears to be intuitive to the subjects (16, 21, 22, 41–48), one of which represented an equal reward distribution and the other an unequal distribution favoring the proposer. The tokens acted essentially like money that could be exchanged for food. Respondents could either accept the offer by returning the selected token to the experimenter or reject it by not returning the token (Fig. 1). Results of the UG were compared with those of a preference test similar to the DG, where the respondent could not influence outcomes. This methodology allowed us to explore whether respondents were sensitive to unequal distributions (by refusing unequal offers) and whether the proposers themselves were sensitive to potential rejections (by altering their choice dependent on their partner’s potential effect on the outcome). In the latter case, proposers, like humans, should make different choices in the UG and DG. We tested human children (ages 3–5 y) with essentially the same token paradigm (for minor experimental differences, see Materials and Methods).

Results

Chimpanzees. Despite initial preferences for the selfish token (binomial tests, all \( P < 0.05 \); see Table 1 for exact two-tailed \( P \) values), all four chimpanzee proposers more often chose the equitable token in the UG condition than in the preference test (exact McNemar’s test, all \( P < 0.05 \); Fig. 2 and Table 1). Two of the four proposers, furthermore, chose the equitable token in the UG significantly more often than expected by chance. During the UG, no respondent ever refused to return an offer, although their behavior might have signaled the potential for them to do so (Discussion).

Thus, chimpanzees, like humans in previous studies, chose a more equitable split of rewards in the UG compared with their choices when their partner had no recourse, as in DGs. The change in choices was apparently spontaneous, occurring without any refusals by the partner and within a small number of trials, making it difficult to ascribe it to learning during the experiment itself. Moreover, this pattern of choices was consistent, with all four individuals showing the same behavioral change. Thus, we found that chimpanzee proposers changed their behavior between two conditions that were identical except for the degree of control given to the recipient, choosing to make more equitable offers when their partner had control.

Children. Children also preferentially selected the selfish token in the preference tests (group-level binomial, \( P = 0.045 \), two-tailed), but they showed no preference for either token in the UG

![Fig. 1. Experimental setup for pairs of chimpanzees following a four-step sequence. Step 1: The proposer (P) is presented with a choice of two tokens, one representing an equal split of the rewards and the other representing an unequal split favoring the proposer. The proposer is free to select either token. Step 2: The proposer passes the selected token to the respondent (R) through a mesh panel. Step 3: The respondent either returns the token to the experimenter to accept the offer, drops the token, or does not return it for 30 s. Step 4: Six banana rewards are visibly divided on a tray in front of the chimpanzees according to the token selected. Here the dots represent an unequal 5:1 distribution of rewards in favor of the proposer. The tray is then pushed within reach of the chimpanzees so that each can collect its reward (s). Note that the experimental setup for children was similar, except that a commercially available baby gate was used to separate the participants and the experimenter.](image-url)
condition (group-level binomial, $P = 0.38$, two-tailed). However, based on results of previous research, we predicted that children would be more equitable in the UG condition than in the preference test (49, 50), and found this to be the case (Mann–Whitney U test, $P = 0.044$, one-tailed). Due to testing constraints, data on children were evaluated in a between-subject design rather than the within-subject design used with chimpanzees. As with chimpanzees, no child ever refused to return an offer. Thus, children also changed their pattern of choices in the UG, despite the absence of refusals by recipients.

**Discussion**

Chimpanzees and children were similarly sensitive to the contingencies of the ultimatum game. In a simple choice task resembling the DG, with either a passive partner (chimpanzees) or while alone (children), both species preferentially chose a “selfish” offer that brought the majority of rewards to themselves. In the UG condition, in contrast, respondents could affect the outcome (by accepting or rejecting the offer), and both species shifted their choices to a more equitable distribution. This shift is similar to the way adult humans change their offers between DGs and UGs (4, 6, 7). Most adult humans are more selfish in DGs than in UGs. Thus, we demonstrated that chimpanzees, like humans, change their distribution choice in the same setting (i.e., paired with a conspecific from their social group) dependent on (i) how their behavior affects a partner and (ii) the potential effect of their partner on the outcome. However, it is unclear whether both of these possibilities affect behavior simultaneously (4) or whether one consideration dominates the decision.

Our findings are in contrast to previous UGs with apes (19, 20). In these studies, the authors concluded that chimpanzees were rational maximizers, making low offers that were mostly accepted. However, the apes also accepted 56% of zero offers in these studies (19). According to the theory of rational maximization, proposers should offer the smallest possible unit of the resource and respondents should accept any nonzero offer, but not zero offers (4, 19). Because the responders failed to follow this rule, they cannot be classified as rational maximizers. Either some other motivation caused them to accept zero offers or they did not fully understand the task (24, 25). The contrast between previous and current studies was probably due to the use of a more intuitive paradigm in the present case (cf. 21).

Neither in the chimpanzees nor in the children did responders ever refuse, where a refusal was defined as failure by the responder to return the offer to the experiernerster within 30 s (25). This is likely because neither species was explicitly trained that refusal was an option (like the chimpanzees, children were not verbally instructed about any of the contingencies). Nonetheless, proposers changed their offers when a partner had control over the reward distribution. We cannot rule out that the proposers were preemptively responding to the potential for refusals, even if these never materialized. In fact, adult humans, who typically offer 50% of the rewards, usually are given only a single choice during any UG experiment, and so have not been punished for making an inequitable decision either. They, too, are presumably responding to the mere potential of refusals. Both chimpanzees and humans have prior real-life experience with inequitable outcomes, which may make them sensitive to the possibility of punishment. For example, chimpanzees who do not share food with others are more likely to encounter threats and temper tantrums (40, 51), and chimpanzees may refuse to share with individuals who did not previously groom them (31), punish theft (52), and protest against both advantageous and disadvantageous inequity in experimental settings (16, 35). Thus, as in humans, social norms may affect performance in this task. Alternatively, because in the UG, cooperation was needed to gain rewards, it is possible that proposers were more generous because they were working with the respondent, because involvement in a task may increase their sensitivity to inequitable outcomes (35). If this were the case, refusals would not be needed to influence their choices.

We observed variation among our pairs of chimpanzees that might be accounted for by their social relationships, although given our small sample size we were unable to reach definitive conclusions. For example, the chimpanzee pair that showed the least equitable behavior (KT–GA) was a mother–daughter pair with the daughter as the proposer. Possibly, their close social relationship made them less sensitive to unequal reward distributions (16, 53). Subsequent studies on how chimpanzees change their choices in a social context should include measures of relationship quality and relative dominance rank.

Even though too rare for quantitative analysis, communicative interactions by respondents to proposers occurred in both children and chimpanzees. Child respondents sometimes made verbal comments about the reward distribution such as “you got more than me” and “I want more stickers.” Chimpanzee respondents occasionally intimidated proposers, whereas proposers never did the same toward respondents. For example, in the chimpanzee pair MS–RT, five instances of threatening behavior were recorded. Three involved RT (respondent) spitting water at MS (proposer). The other two involved RT hitting the mesh barrier separating her from MS when the latter was about to pass a token. Although we found no statistically significant connection between offers made and threats received in the chimpanzees, likely due to the rarity with which they occurred, these negative reactions might have influenced the proposer. In a previous study, attention-getting behavior by a partner increased the actor’s prosocial tendencies, suggesting that social interactions may influence decisions in experimental tasks (21). In both children and chimpanzees, the respondent’s behavior may have cued the proposer that a negative response was possible. Thus, even though the mechanism behind these choices is unclear, chimpanzees appear to show the same sensitivity as do children to the attitude of others during resource division. Their interest in fair distributions probably helps them reap the benefits of cooperation.
Materials and Methods

General Method. Before testing, individuals were trained on the contingencies of the task. See below for the training details of each species. After training, subjects were brought into the testing environment in pairs. The proposer was presented with a choice between two differently colored tokens, each representing a different offer. We chose to use tokens representing food rather than food directly to prevent their choices from being influenced by prepotent responses to seeing food (20). Additionally, this is more similar to human UGs, where money is used (often with a computer interface and time delay between the subject’s choice and the actual payoff). Money and tokens both have an abstract value (i.e., can be used in the future to acquire goods) and should therefore reduce prepotent responses. Here one token represented an equal split of the six pieces of reward (3:3), whereas the other token favored the proposer at a 5:1 ratio. The proposer selected a token and passed it to the respondent. The respondent could either return the token to the experimenter, thus accepting the offer, or refuse to return the token, hence rejecting the offer. If the token was returned, both individuals were given the proposed split of the reward. Our design stipulated that if the respondent failed to return a token for 30 s, no rewards would be distributed, but this never occurred (Fig. 1). Choices in the UG were then compared with choices in a preference test reminiscent of a DG, in which there was no possibility for action by the respondent, to determine whether offers varied if the partner lacked control over the reward distribution.

One goal of this study was to test chimpanzees and children using similar methods to variable value rewards as is done with human children to verify that humans responded to this design as anticipated based on other UG designs. To keep the tests as similar as possible, children were tested with a peer from their social group (e.g., their preschool class) using an exchange procedure learned with limited verbal instruction from the experimenter. We also gave them repeated UG trials, in case the repetition changed behavior (most UG experiments with verbal instruction from the experimenter. We also gave them repeated UG trials, in case the repetition changed behavior (most UG experiments with verbal instruction from the experimenter). All trials, in case the repetition changed behavior (most UG experiments with verbal instruction from the experimenter).

Chimpanzee Subjects. We tested six adult chimpanzees (P. troglodytes) at two research facilities (n = 4 female chimpanzees at the Yerkes National Primate Research Center Field Station (YFS); n = 2, one male and one female chimpanzee at the Language Research Center, Georgia State University (LRC)). All apes were socially housed and had access to both indoor and outdoor enclosures. At all sites, chimpanzees were fed a diet of chow and fresh fruits and vegetables in addition to any food they earned during testing. Water was available ad libitum. No animals were food- or water-deprived for this study. The Institutional Animal Care and Use Committee of each institution approved this research.

Chimpanzee Pretesting. Before testing, chimpanzees were required to pass a number of controls. These ensured that we could assume that the motivation and behavior of chimpanzees’ behavior were similar to those seen in humans. To be included in the study, chimpanzees had to (i) be able to pass a token to another chimpanzee; (ii) have no initial preference for the tokens; (iii) be able to discriminate between the reward quantities; (iv) be trained on the value of the tokens with a passive and naive partner who was rewarded according to the token selection, and (v) show that they preferred to keep the token that brought them the largest reward (indicating that they understood the relative token values) when a passive and naive partner was present. First, because the chimpanzees would have to pass a token from one enclosure to another in the preference and UG tests, individuals who had not previously been trained to exchange tokens for rewards (those from the YFS) were given such training (LRC chimpanzees had such training (44)). They were placed in two adjacent testing rooms separated by a mesh panel that allowed full visual and auditory contact as well as limited tactile contact (e.g., limited grooming). One experimenter then sat in the enclosure adjacent to the chimpanzee, and a second experimenter outside of the enclosures handed a token to the chimpanzee. The first experimenter then attracted the attention of the chimpanzee through vocalizations and gestures. If the chimpanzee passed the token to this person, they were rewarded with a banana slice by the experimenter who had given them the token. After 10 successful trials, the experimenter to whom the chimpanzee gave the token began returning it to the experimenter who was outside of the enclosure. This experimenter then rewarded both the chimpanzee and the other experimenter with a slice of banana. We then replaced the second experimenter with a chimpanzee. After chimpanzees completed 10 consecutive passes on each of 2 separate days to another chimpanzee, they were considered trained. Next, chimpanzees had to pass an initial preference test with the tokens that represented offers. This was done to ensure that no chimpanzee had a bias toward one token before training occurred. We presented these tokens on a tray to the chimpanzee, who could then touch either token. As soon as one token was touched, the tray was removed and the tokens were counterbalanced for the next trial. Each chimpanzee was given one session of 12 trials. No rewards were given for either token during this test to avoid reinforcement for either token. No individual had a greater than 75% preference for either token (average preference for preferred token, 6.625 out of 12).

Chimpanzees were not tested on whether they could discriminate between the quantities to which they would be exposed in the experiment. We used six pieces of a high-quality food item (~1-cm-thick banana slices) as the pot that was to be split. The chimpanzees could make one of two offers: 3:3 or 5:1 in their own favor. Thus, animals in the proposer role received preference tests on the quantities of 5 vs. 1 and 5 vs. 3 (to ensure they were sensitive to the contrast between their potential rewards). Animals in the respondent role received preference tests on the quantities of 5 vs. 1 and 3 versus 1. Animals passed the preference test if they selected the larger quantity on at least 18 out of 24 trials in two 12-trial sessions given on different days (binomial test, P ≤ 0.02). Animals were given up to 10 sessions to reach these criteria.

Finally, chimpanzees were trained to understand what their partners would receive for each of the token choices. Each chimpanzee was paired with a “foil” partner chimpanzee who was not used in the subsequent experiment, who was naive to the conditions of the task, and who did not participate in the training trials except as a passive recipient. We used an untrained individual to decrease the likelihood of behavioral responses to the subject’s token choice, which potentially could have influenced offers.

As in the UG, the six rewards were lined up on a tray in front of the chimpanzees. The subject chimpanzee was given a choice between two tokens to return to the experimenter (they did not pass the offer to the foil chimpanzee). The tokens were presented via a vertical peg board with eight possible token locations. Actual locations were randomized for each trial. The rewards were then divided according to the offer indicated by the chosen token and presented to the chimpanzees. Chimpanzees had to demonstrate a preference for the 5:1 option on at least 18 of 24 choices (binomial test, P ≤ 0.02; see Table 2 for individual data) in two consecutive sessions. Subjects were given 12 trials a day for up to 10 d; LRC chimpanzees passed this pretest on the first day. All chimpanzees, taking an average of 2.5 sessions compared with 6.75 sessions.

Chimpanzee Test Procedure. During the test phase, all six rewards were lined up on a tray in front of the chimpanzees. The subject chimpanzee was given a choice between two tokens to return to the experimenter (they did not pass the offer to the foil chimpanzee). The tokens were presented via a vertical peg board with eight possible token locations. Actual locations were randomized for each trial. The rewards were then divided according to the offer indicated by the chosen token and presented to the chimpanzees. Chimpanzees had to demonstrate a preference for the 5:1 option on at least 18 of 24 choices (binomial test, P ≤ 0.02; see Table 2 for individual data) in two consecutive sessions. Subjects were given 12 trials a day for up to 10 d; LRC chimpanzees passed this pretest on the first day. All chimpanzees, taking an average of 2.5 sessions compared with 6.75 sessions.

Table 2. Chimpanzee performance on quantity preference tests

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All chimpanzees passed pretests, demonstrating that they could discriminate between quantities and preferred the token worth the larger quantity in a non-UG context (i.e., when there were no negative consequences for such a choice).

*Denotes significant difference from chance; binomial test, P < 0.01.
All test sessions were recorded on a digital video camera and later coded by a coder who was not involved with the experiment and was blind to the condition that the child was assigned. Interrater reliability for choice was obtained for 20% of the sessions. Interrater reliability for choice and whether the offer was returned to the experimenter was 100% (Cohen’s κ = 1, P < 0.001).

Human Subjects. Twenty children from two preschools in the southeastern United States (n = 20, 9 males, 11 females; age range, 2–7; mean age, 3.8 y; SEM, 0.36) were tested with other individuals from their class in the UG task. We were allowed to test these children for only a single test session, and so could not perform the preference test on a different day. To avoid the possibility that the exposure to rewards in one task would affect responses in the other if they were performed immediately subsequently, 10 children were separately brought into a laboratory at Georgia State University to determine what reward distribution they preferred when they were alone (7 females, 3 males; age range, 3–4 y; mean age, 3.8 y; SEM, 0.13). This was similar to the token preference test in chimpanzees and allowed us to get group preferences without the potential bias of previous exposure. For all testing, children were seated on the opposite side of a commercial baby gate from the experimenter, to mimic the separation between subjects and experimenter in the chimpanzee studies. Prior to the experiment, we obtained informed consent from a parent. The Institutional Review Board at Georgia State University approved this research.

Human Pretesting. All children were trained on the tokens and associated offers immediately before the experiment. The proposer was given a token representing one of the two offers. Rewards (stickers) were laid out in front of the barrier so that the children could see but not reach them. Children were instructed to pass the selected offer to their partner around the barrier. The partner could then return the offer to the experimenter. To indicate to the child that they could return the offer, the experimenter extended her hand palm up toward the child (a similar gesture was used to indicate the possibility of exchange with chimpanzee responders). No verbal instructions were used to get subjects to return the offer. The children were then rewarded according to the offer returned. Children received a total of four forced-choice training trials, two for each offer. During training the experimenter talked to the children to build rapport. However, besides the limited instructions given, the experimenter did not talk about the task. If the children asked the experimenter a direct question about the task, the experimenter would respond by saying, “What do you think?” or by shrugging her shoulders.

Human Preference Test. Children participating in the preference test condition were tested at a laboratory at Georgia State University. Training and testing procedures were similar to those used in the UG, although with two differences, due to their being tested alone. During both training and the preference test, children returned the offer directly to the experimenter. They were rewarded with the selected offer as in the UG, but the portion of the reward that would have gone to a partner was removed from the testing area. Thus, the preference test was similar to the individual preference test given to chimpanzees, with the exception that in the chimpanzee tests, there was always a naive conspecific partner present.

Human Test Procedure. The test procedure was identical to the training protocol, except that one of each token was presented to the proposer. That child could then choose which offer to select. If a child tried to take both tokens, they were removed and replaced while the experimenter said “which one?” The proposer then passed the token to the respondent, who could return the token to the experimenter. If the token was returned (which was always the case in our study), the children were rewarded according to the offer represented by the returned token. Children were given one session of eight trials.

All test sessions were recorded on a digital video camera and later coded by a coder who was not involved with the experiment and was blind to the conditions and hypotheses. Interrater reliability was obtained for 20% of the sessions. Interrater reliability for token choice and whether the token was returned to the experimenter was 100% (Cohen’s κ = 1, P < 0.001). With the chimpanzee tokens, two-tailed P values were used except when comparing the children’s performance in the experimental test to the preference test. In this case, one-tailed P values were used based on our prediction that children would behave similarly to children and adults in previous studies (49, 50).

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