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Children, but not great apes, respect ownership

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Highlights

- Ownership can be viewed as a cooperative arrangement where individuals inhibit their tendency to take other's property
- Dyads of captive apes and human children could access the same food resources
- Human children, but not apes, respected their partner's claims
- This highlights the uniquely cooperative nature of human ownership arrangements

Abstract

Access to and control of resources is a major source of costly conflicts. Animals, under some conditions, respect what others control and use (i.e., possession). Humans not only respect possession of resources, they also respect ownership. Ownership can be viewed as a cooperative arrangement, where individuals inhibit their tendency to take others' property on the condition that those others will do the same. We investigated to what degree great apes follow this principle, as compared to human children. We conducted two experiments, in which dyads of individuals could access the same food resources. The main test of respect for ownership was whether individuals would refrain from taking their partner's resources even when the partner could not immediately access and control them. Captive apes ($N = 14$ dyads) failed to respect their partner's claim on food resources and frequently monopolized the resources when given the opportunity. Human children ($N = 14$ dyads), tested with a similar apparatus and procedure, respected their partner's claim and made spontaneous verbal references to ownership. Such respect for the property of others highlights the uniquely cooperative nature of human ownership arrangements.

Keywords: conflict, cooperation, ownership, social behaviour, apes, children

Children, but not great apes, respect ownership

Ownership can be described as a relation between individuals with regard to an object and some have argued that ownership relations are based on cooperative arrangements that specify owners' rights and duties (Christman, 1994; Hume, 1739/2000; Rose, 1985; Singer, Berger, Davidson, & Penalver, 2017). In other words, ownership is viewed as a set of mutually recognized and respected norms regulating how people relate to objects (Kalish & Anderson, 2011; Snare, 1972). For instance, individuals will inhibit their tendency to take away others' property on the condition that others will do the same. Importantly, ownership in this view is distinct from possession as it does not (necessarily) rely on physical contact or close proximity to an object. An owner can thus trust others to respect her property even when she does not currently possess it or when she is absent.

In humans, understanding of ownership emerges early in ontogeny: Toddlers already infer ownership of their own objects as well as ownership of present and absent owners (Fasig, 2000; Gelman, Manczak, & Noles, 2012; Brownell, Iesue, Nichols, & Svetlova, 2013). They also verbally claim ownership of and win fights over their own toys irrespective of current possession (Ross, 1996; Ross, Conant, & Vickar, 2011; Ross, 2013; Ross, Friedman, & Field, 2015). Preschoolers prioritize statements of verbal ownership over physical possession (Blake, Ganea, & Harris, 2012) and give priority to owners in conflicts about the use of objects (Neary & Friedman, 2014). Furthermore, preschoolers signal ownership of objects to absent others, respect what belongs to absent owners, and actively enforce their own and other's ownership claims (Rossano, Rakoczy, & Tomasello, 2011; Kanngiesser & Hood, 2014; Rossano, Fiedler, & Tomasello, 2015). Taken together, this evidence shows that young children have a notion of ownership as distinct from possession or current use.

There is some indication that respect for ownership claims overrides young children's tendencies to accumulate resources. When given windfall resources to share with others, young children usually give away little and keep the biggest share to themselves (Rochat et al., 2009; Cowell et al., 2017; for reviews, see: Gummerum,

Hanoch, & Keller, 2008; Ibbotson, 2014; McAuliffe, Blake, Steinbeis, & Warneken, 2017; Blake, 2018). However, toddlers share more resources with peers if there are cues to ownership such as colours and spatial arrangements (Ulber, Hamann, & Tomasello, 2015). Preschoolers also share equally after they have acquired resources collaboratively (Warneken, Lohse, Melis, & Tomasello, 2011; for a review see: Warneken, 2018) - likely because they view the resources as jointly owned. In addition, preschoolers share toys more frequently if they are told that the toys belong to the class (Eisenberg-Berg, Haake, Hand, & Sadalla, 1979). While children view their ownership claims on their own resources as categorical, their respect for others' ownership claims varies with the strength of those claims (i.e., whether resources were found or made; Davoodi, Nelson, & Blake, 2018).

It has been suggested that humans and animals share a sense of ownership (Sherratt & Mesterton-Gibbons, 2015; Stake, 2004; Gintis, 2007). Many animals occupy territories or take possession of resources, and access to and control of resources is a major source of costly conflicts. It has been observed for many taxa that first possessors of resources often defeat intruders (Kokko, López-Sepulcre, & Morrell, 2006) and, in some instances, even remain unchallenged (Sigg & Falett, 1985; Kummer & Cords, 1991). Respect for first possession can prevent protracted and escalated conflicts (Smith & Price, 1973), though the precise mechanisms underlying it are debated (Grafen, 1987; Kokko et al., 2006; Sherratt & Mesterton-Gibbons, 2015). One key factor appears to be an individual's constant use or physical control of the contested resources (Kummer, 1991; Tibble & Carvalho, 2018).

Apes show some possession-related behaviours (Kummer, 1991; Brosnan, 2011). For example, chimpanzees occupy territories that they regularly patrol and defend against intruders (Mitani, Watts, & Muller, 2002), and great apes value food they currently possess (Brosnan et al., 2007; Kanngiesser, Santos, Hood, & Call, 2011). There is, to date, no experimental evidence on respect for possession in apes and only scarce evidence from other primates: dominant male baboons respect sub-dominant males' possession of food (but respect did not occur in other sex-pairings; Sigg & Falett,

1985); dominant long-tail macaques respect sub-dominants' possession of movable food containers (but not of stationary ones; Kummer & Cords, 1991), and rhesus macaques prefer a food option that is not physically attached to or near a human experimenter (Russ, Comins, Smith, & Hauser, 2010).

All the behaviours described in the previous paragraph relate to physical possession and there is to date no conclusive empirical evidence to support the claim that primates also have a notion of ownership (Sherratt & Mesterton-Gibbons, 2015; Stake, 2004; Gintis, 2007). For example, previous studies (Sigg & Falett, 1985; Kummer & Cords, 1991) allowed for physical control of the contested resource as well as for physical interaction between individuals. It is thus unclear whether the observed respect for possession occurred due to respect of the other's claim, due to fear of immediate retaliation and risk of injury (Sigg & Falett, 1985) or because the possessor simply had the opportunity to escape with the resource (Kummer & Cords, 1991).

We therefore conducted a study with bonobos and chimpanzees (henceforth apes), in which we prevented (i) physical contact with the resource and (ii) physical interactions between individuals. Dyads of individuals were tested in separate testing rooms and had access to an apparatus (placed between the two rooms), where they could harvest food items. We attempted to establish a sense of ownership through the investment of work effort into harvesting items (Kanngiesser, Gjersoe, & Hood, 2010; Kanngiesser & Hood, 2014; Rochat et al., 2014). Each individual worked for two items by pushing the items along transparent tubes to drop them onto trays. To facilitate tracking of the items, the two items were wrapped in the same colour (with distinct colours on each side of the apparatus). Both individuals then had access to the same food items and could retrieve them by pulling the trays to their side. In the simultaneous condition, we gave both individuals immediate access to the rewards. In the delayed condition, we gave one individual immediate access to the rewards, while the other individual had to wait for 45 seconds. The delayed condition was the main test of respect for ownership, as it gave individuals with prior access the opportunity to maximize their own outcome by disrespecting their partner's claim and retrieving all

four items. For comparison, we tested human four-year-olds with a similar apparatus and procedure (Study 2). We selected this age group to ensure that children could operate the apparatus easily and with little training. Moreover, four-year-olds are able to use visual markers to track ownership (Gelman, Manczak, Was, & Noles, 2016) and consider owned objects as non-fungible (McEwan, Pesowski, & Friedman, 2016).

Study 1 - Apes

Methods

Subjects. Eight chimpanzees (*pan troglodytes*) and seven bonobos (*pan paniscus*) participated in the study (for details, see Supplementary Information, Table S1). Three chimpanzees came from a group of eight individuals (B group) and five chimpanzees from a group of 17 individuals (A group); all bonobos came from the same group of ten individuals (C group). In the main test, apes were paired with individuals from the same social group. All apes, except one bonobo, participated twice in the study - each time with a different partner. This resulted in a total of 14 dyads (eight chimpanzee dyads, six bonobo dyads; see Supplementary Information, Table S1, for more information). Individuals were always paired with a partner that differed in social rank (for details, see dominance measure below). Fifteen additional chimpanzees started the training for this study, but were excluded because they were unwilling to participate (12 individuals) or did not pass the training (three individuals). The final sample size was thus determined (i) by the number of apes available at the zoo and (ii) by the number of apes who passed the initial training.

The apes were housed at the Wolfgang Köhler Primate Research Center (WKPRC) at the zoo of Leipzig, where they had access to semi-natural indoor and outdoor enclosures and received regular enrichment. They were fed a variety of fruits and vegetables, occasionally supplemented by animal protein (meat, eggs, and yoghurt). Apes had access to water *ad libitum* and were never food deprived. All apes participated in a variety of studies on a daily basis. Testing took place in the apes' sleeping rooms between 8:30 and 12:30 and participation was entirely voluntarily.

The study was non-invasive and strictly adhered to the legal requirements in Germany. No medical, toxicological or neurobiological research of any kind is conducted at the WKPRC. The study was ethically approved by an internal committee at the WKPRC (committee members: Prof. M. Tomasello, Dr. J. Call, Dr. D. Hanus, veterinarian Dr. A. Bernhard, head keeper F. Schellhardt, and assistant head keeper M. Lohse). Animal husbandry and research comply with the “EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria”, the "WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums" and the "Guidelines for the Treatment of Animals in Behavioral Research and Teaching" of the Association for the Study of Animal Behavior (ASAB). Approval by an Institutional Review Board (IRB) was not necessary as, according to German law (TierSchGes §7 and §8), the use of animals in purely behavioural or observational studies requires no special permission.

Apparatus and materials. Apes harvested food rewards by pushing them along a transparent tube until they dropped on a sliding tray (see Figure 1). They could then retrieve the rewards by opening a door and pulling on a string connected to the tray. All tubes were transparent and rewards always moved in straight lines to allow apes to easily track them (for a detailed description of the apparatus, see Supplementary Information, section 1.2).

We used half a food pellet as reward and wrapped each reward in packing paper. The packing paper made it more effortful for the apes to push the reward along the tube, and allowed us to wrap the rewards in different colours (without having to dye the actual food). In the test sessions, one individual in a dyad always harvested rewards wrapped in blue paper, the other individual always harvested rewards wrapped in red paper. The different colours were introduced to help individuals track their rewards.

Design. Apes first participated in individual training sessions to familiarize them with the apparatus (for details on the training procedure, see Supplementary Information, section 1.3). Only apes that successfully completed the apparatus training participated in the test sessions where they were paired with another individual from

the same social group.

We tested ape dyads in two conditions in a within-subject design. In the simultaneous condition, both individuals could simultaneously access the rewards on the sliding trays. In the delayed condition, one ape had immediate access to the rewards, while the other was blocked for 45 seconds. Each dyad took part in four test sessions of four trials each. The order of test sessions followed an A-B-B-A design: simultaneous session, delayed session, delayed session, simultaneous session. The simultaneous condition always took place in session 1 to give apes experience with the dyadic test situation (i.e., that the other individual harvested rewards and could access the trays, too). We decided to do this as part of the main test to avoid conducting training sessions with social partners (human or con-specific).

Procedure. The study was conducted by two experimenters who baited the apparatus, passed the poking sticks to the apes, removed the barriers from the doors and reset the apparatus after each trial. During test trials the experimenters always turned their backs to the apes once they had removed the barrier (to avoid cueing apes).

In the test phase, apes were paired with an individual from the same social group. Each individual in a dyad was assigned to one of the testing rooms (room 1 or 2) and stayed in the same room during all test sessions of this dyad. In addition, each ape was assigned one reward colour (red or blue). Importantly, the hydraulic door between the two room was closed to prevent apes from directly interacting with each other.

In the simultaneous condition, we baited two tubes in each room (e.g., tubes 1 & 3 in room 1, and tubes 2 & 4 in room 2, order counterbalanced across trials), so that all four tubes were baited. Once both apes had pushed the rewards onto the trays, the grey barriers on each side of the apparatus were simultaneously removed by E1 and E2 so that both apes had simultaneous access to the trays.

In the delayed condition, the set up was the same except that we used one gray and one yellow barrier. The individual on the side with the yellow barrier was blocked from accessing the trays for 45 seconds, while the individual on the side with the gray barrier had immediate access to the trays. We alternated the side of the yellow barrier

between trials, so that each ape was blocked on two of the four trials per session. We counterbalanced across delayed sessions which ape was blocked first.

Dominance measure. To obtain a dominance measure, we presented keepers with all dyad combinations for each ape-group and asked them to indicate (yes/no) the dominant individual in each dyad. We received ratings from four keepers of the chimpanzee A group, from three keepers of the chimpanzee B group and from three keepers of the bonobo group. We used the ratings to select dyads for the study, in which one individual was rated as dominant by all (or the majority of) keepers.

Data coding. We recorded all training and test sessions with two cameras that were focused on the right and the left side of the apparatus, respectively. Apes' performance during training and test sessions was live-coded by the third author (R. F.) and confirmed from video-recordings. For the test sessions, we coded which sliding trays apes pulled to their side. 28 trials (18 chimpanzee trials, 10 bonobo trials; 13% of all trials) had to be repeated because of apparatus failure or experimenter error. One bonobo dyad (B3) did not complete the last test session (simultaneous condition) because one individual refused to participate. For reliability purposes, a second coder re-coded the test sessions (valid trials only) of four dyads (two bonobo and two chimpanzee dyads; 29% of dyads). Agreement between coders was perfect (Cohen's $\kappa = 1$).

Data analyses. All data analyses were conducted in R Version 3.4.1. (for details, see Supplementary Information). We analyzed the data using Generalized Linear Mixed Models with a binomial error distribution. In the GLMM, we entered the response variable as a matrix of the number of the owner's items that were retrieved by the owner (left column; range = 0 - 2) and by the non-owner (right column; range = 0 - 2), respectively. The matrix variable represents the proportion of the owner's items that were correctly retrieved by the owner while considering the discontinuous nature of the response variable (see Baayen, 2008, p. 197). The model estimates have the exact same interpretation as in any other logistic model. We entered as fixed effects: condition, species, and their two-way interaction. We entered as control predictors: session

number, trial number, dominance of the owner, and sex of the owner. We also included random intercepts and random slopes (for details, see Supplementary Information, section 1.4). We conducted model comparisons to determine the model with the best fit to the data and determined the p-values for each fixed effect by conducting likelihood ratio tests (for details, see Supplementary Information, section 1.4).

We further used GLMM analyses (of the reduced model) to test for each species whether the proportion of own items retrieved by owners differed from chance. We made use of the fact that the model estimate for the intercept and the associated p-value indicate whether the proportion of own items is significantly different from chance levels. The intercept reveals the expected mean of the response variable for each reference level of the factor, in this case species, and all other predictors being zero. However, due to the nature of logistic models, there might be a small difference between the sample mean assumed by the model and the actual sample mean, for which we adjusted (for details, see Supplementary Information, section 1.4).

Results and discussion

Comparison of the full model to a null model (without condition and species and their two-way interaction) showed a trend for improvement in model fit for the more complex model, $\chi^2(3) = 6.914$, $p = 0.075$. Likelihood ratio tests revealed that none of the fixed effects in the full model reach significance at the 0.05 level (for details, see Supplementary Information, Table S2). Next, we fitted a reduced model with the main effects of condition and species (and without their two-way interaction). Comparison of the full model to the reduced model revealed no significant improvement in model fit for the more complex model, $\chi^2(1) = 2.215$, $p = 0.137$. The reduced model revealed a significant effect of species, $\chi^2(1) = 4.614$, $p = 0.032$; no other predictors were significant (for details, see Table 1).

Figure 2 provides details on the proportion of own items retrieved by bonobos and chimpanzees. In the simultaneous condition, bonobos retrieved an average proportion of $M = 0.42$ ($SD = 0.15$) own items and chimpanzees of $M = 0.54$ ($SD = 0.08$) own

items. In the delayed condition, bonobos retrieved an average proportion of $M = 0.49$ ($SD = 0.04$) own items and chimpanzees of $M = 0.50$ ($SD = 0.03$) own items (see Supplementary Information, Table S3 and S4, for further details). We used GLMM analyses (of the reduced model) to test for each species whether the proportion of own items retrieved by owners differed from chance. Intercepts revealed that apes failed to retrieve their own items at levels that differed significantly from chance (bonobos: Est = -0.185, SE = 0.211, $Z = -0.879$, $p = 0.380$; chimpanzees: Est = 0.086, SE = 0.164, $Z = 0.525$, $p = 0.600$). This shows that, in both conditions, apes were as likely to retrieve their partner's items as they were to retrieve their own.

In the delayed condition, individuals with prior access retrieved all of the available food in the majority of trials (bonobos: 85% of trials; chimpanzees: 95% of trials; see Fig. 3), maximizing their own outcome. In the simultaneous condition, the distribution of food within dyads was either equal (bonobos: 70% of trials; chimpanzees: 39% of trials) or unequal (bonobos: 30% of trials; chimpanzees: 53% of trials).

In summary, we found that neither bonobos nor chimpanzees retrieved their own items at levels that differed significantly from chance. Moreover, when given the opportunity to monopolize food in the delayed condition, individuals from both species took all available food on the vast majority of trials. We found a significant species difference, which seems to be driven primarily by two bonobo dyads who, in the simultaneous condition, often retrieved their partner's items instead of their own. Individuals in these two dyads had one of the largest age differences (9 and 11 years, respectively) in the ape sample and it is possible that this influenced their food retrieval. Furthermore, bonobos achieved an equal reward division more often than chimpanzees (70% vs. 39%) in the simultaneous condition. Some studies have found that chimpanzees monopolize food more frequently than bonobos in feeding contexts (Hare, Melis, Woods, Hastings, & Wrangham, 2007; Wobber, Wrangham, & Hare, 2010) - though, there is an ongoing debate about whether such findings reflect species differences in sociality (see e.g., Jaeggi, Stevens, & van Schaik, 2010, for a discussion). We used food items in our study for the most stringent test of respect for ownership as

apes are usually strongly motivated by food. Studies have shown that apes behave differently towards food and non-food items (such as toys or tools) in their possession: they are reluctant to give up food for food of similar value, but frequently trade non-food items (Brosnan et al., 2007; Kanngiesser et al., 2011) - unless they can be directly used to acquire food (Brosnan, Jones, Gardner, Lambeth, & Schapiro, 2012). Regarding our study set-up, we predict that apes would take non-food items indiscriminately of who had initially harvested them.

Study 2 - Human children

In Study 2, we tested four-year-old human children with an apparatus and procedure similar to Study 1. We did not use ownership labels during testing to avoid establishing ownership verbally.

Methods

Participants. 28 four-year-old children (*Mean age* = 4 years 7 months, *SD* = 4 months, *Range* = 48 - 60 months; 14 female) took part in the study. Children were paired in same-gender dyads (14 dyads in total). Since the ape study was conducted first, the sample size of this study was chosen to match the sample size of Study 1. Seven additional children were trained on the apparatus but did not participate in the study because they were absent on the testing day(s). Children were recruited from a database of parents who had signed up their children as participants in developmental studies. Testing took place in children's kindergarten (six kindergartens in total). Children came mostly from middle-class families and lived in a city in Eastern Germany with more than half a million inhabitants.

The study was conducted in accordance with the Declaration of Helsinki and the ethical guidelines of the German Psychological Society (DGPs) and the Association of German Professional Psychologists (BDP). The study did not involve any invasive techniques, ethically problematic procedures or deception, and, therefore, did not require approval by an Institutional Review Board (see the regulations on freedom of research in the German Constitution, § 5 (3)).

Apparatus and materials. We used an apparatus that was similar to the one in study 1. Children worked for rewards (gummy bears) by pushing them along a transparent tube until they dropped on a sliding tray (see Figure 4). They could then retrieve the rewards by opening a door and pulling on a string connected to the tray. All tubes were transparent and rewards always moved in straight lines to allow children to easily track the rewards (for details on the apparatus, see Supplementary Information, section 2.1).

We used gummy bears as rewards and placed them in small containers. The containers allowed us to handle the food in a hygienic way, and to mark the containers in different colours. In the test sessions, one child always had green-dotted containers on their side, and the other child always had blue-dotted containers on their side to help them track their rewards.

Design. Children first participated in individual training sessions to familiarize them with the apparatus (day 1). Then, they participated in test sessions where they were paired with another child of the same gender. We tested dyads of children in two conditions in a within-subject design. In the simultaneous condition, both children could simultaneously access the rewards on the trays. In the delayed condition, one child had immediate access to the rewards, while the other was blocked for 45 seconds. Each dyad took part in four test sessions of four trials each. The order of test sessions followed an A-B-B-A design: simultaneous session, delayed session, delayed session, simultaneous session. The simultaneous condition always took place in session 1 to give children experience with the dyadic test situation and to avoid training sessions with a social partner. We decided to use the same A-B-B-A design as in study 1 to allow for comparability with the ape data. We conducted two test sessions per day to reduce the number of testing days for children. On day 2, children took part in one simultaneous and one delayed session, and on day 3 they took part in one delayed and one simultaneous session. The training day (day 1) and the two testing days (day 2 and 3) took place within a four-day window with a maximum of a one-day break between the training and the first testing day (testing days 2 and 3 always took place on consecutive

days).

Procedure. The study was conducted by an experimenter (E1) and a helper (E2). E1 was in the room with the children during trials, passed them the poking sticks and unblocked the doors. During the test trials, E1 always turned her back to the children while they pulled on the trays (to avoid cueing children). In between trials, E2 supervised the children outside the room, while E1 prepared the apparatus for the next trial.

Only children who successfully completed the apparatus training participated in the study (for details see, Supplementary Information section 2.2). During training, we used unmarked, yellow containers for the rewards. In the training and test sessions, E1 did not use any possessive pronouns (e.g., *deins* 'yours') when talking about the rewards or the apparatus to avoid verbal priming of ownership.

Dominance measures. Before the test sessions on day 2, children participated in a dominance test with their peer-partner. The partner was of the same-gender and came from the same kindergarten group; s/he remained the same for all test sessions. The two children sat on the floor and E1 placed a box between them announcing that it contained a surprise-toy (a toy mobile phone). Then E1 went to a corner of the room and turned away from the children. Children had 1 minute to open the box and play with the toy. In addition to this behavioural dominance measure, we asked the children's kindergarten teachers which child in a given dyad was the dominant child (teacher ratings are available for all dyads except two).

Test. Children participated in the test with their peer-partner. Each child was assigned to one side of the apparatus and stayed on that side during all test sessions. In addition, each child was assigned one reward container colour (green or blue). Children collected their gummy bear rewards in lunch bags marked with their names.

In the simultaneous condition, we placed rewards in two tubes on each side of the apparatus (e.g., tubes 1 & 3 on one side, and tubes 2 & 4 on the other side, order counterbalanced across trials), so that all four tubes contained rewards. At the start, E1 handed children the sticks and asked them to start. Once children had pushed all

reward containers onto the trays, E1 collected the sticks, unblocked the doors on both sides of the apparatus and turned away. Children could then retrieve the rewards by pulling the trays (if necessary E1 assisted with opening the reward containers at the end of the trial). Then, children left the room and E1 prepared the apparatus for the next trial.

In the delayed condition, the set up was the same except that we used the stop-sign and the hour glass. The child on the side with the stop-signed was blocked from accessing the trays for 45 seconds, while the child on the other side had immediate access to the trays. Before the start of the first trial, E1 reminded children that the doors would be blocked for some time on the side with the stop-sign; E1 also told children that they were not allowed to switch sides. After the children had pushed the rewards onto the trays, E1 unblocked the doors on the side without the stop sign, turned over the hour glass and turned away. After 45 seconds E1 unblocked the doors on the side with the stop-sign. We alternated the side of the stop-sign between trials, so that each child was blocked on two of the four trials per session. We counterbalanced across delayed sessions which child was blocked first.

Data coding.

Reward retrieval. All training and test sessions were videotaped. We scored from videotape (1) which reward containers children retrieved by pulling the trays to their respective sides, and (2) the final distribution of reward containers after some children had exchanged or handed over reward containers. All data was coded by the fourth author (A.T.). For reliability purposes, a second coder re-scored children's behaviour for four dyads (two female dyads and two male dyads; 29% of dyads) from videotape. Agreement between the two coders for retrieval was perfect (Cohen's $\kappa = 1$) as was agreement for the final distribution of rewards (Cohen's $\kappa = 1$).

Dominance measure. To determine dominance, coder 1 scored from videotape which child in a dyad took the toy first (scored as 1); in one dyad no child took the toy, so we scored which child opened the box first. We also scored which child in a dyad played the longest with the toy (scored as 1). In addition, kindergarten

teachers were asked to rate which child in a dyad they viewed as dominant (scored as 1). We combined these three measures to calculate a dominance score (0-3; for two dyads without teacher rating the score was 0-2). The child with the highest score in a dyad was rated the dominant child. We opted for this binary dominance measure to ensure comparability with the binary dominance measure in study 1. For reliability purposes, coder 2 re-scored children's dominance behaviour for four dyads (two female dyads and two male dyads; 29% of dyads) from videotape. There was only moderate agreement between the coders regarding the dominance scores (Cohen's weighted $\kappa = 0.684$) - mainly because the primary coder had accidentally swapped two children when coding the play duration. We consequently had a third coder check all dominance interactions again from videotape. We corrected the dominance scores of five dyads, for two of which we had to correct the binary dominance measure.

Verbal behaviour. Children's utterances during the test sessions were first transcribed verbatim (by coder 3). Next, we categorized children's utterances in the retrieval phase, that is, we only consider utterances from the moment E1 unblocked the doors to the moment both children had retrieved all rewards and started putting them in their bags. We focused on this phase because it was the most informative in terms of children's spontaneous talk about the rewards. Each utterance was scored by a fourth coder who scored whether children referred to ownership, container-colour, reward-allocation, fairness or protested (Note that each utterance could be scored in more than one category):

- **Ownership:** Children referred to ownership of reward containers and/or rewards (gummy bears) using possessive pronouns (e.g., *meins* 'mine', *deins* 'yours') or other forms of explicitly stating ownership in German (e.g., *Das gehört mir* 'This belongs to me'). Utterances referring to ownership of sides (e.g., *Das ist auf meiner Seite* 'This is on my side') were not scored as they do not directly refer to ownership of the rewards. Utterances including the word *haben* 'have' (e.g., *Ich hab viele* 'I have many') were also not scored, as they may only indicate temporary possession and do not unambiguously refer to ownership.

Examples: *Ich nehm meine Blauen!* 'I take my blue ones'; *Du darfst nicht meine machen* 'You are not allowed to take mine'. *Du hast deinen Grünen* 'You have your green one'

- **Colour:** Children referred to the colour of the blue or green reward container. Utterances that mentioned colours but did not refer to the reward containers (e.g., *Grün heißt green in Englisch* 'Grün means green in English'; *Das ist meine Lieblingsfarbe* 'This is my favourite colour') or that referred to colours other than green or blue were not scored.

Examples: *Ich hab blau* 'I have blue'; *Wer auf der Seite ist, hat grün* 'The one this side has green'; *Du musst doch den blauen nehmen* 'You have to take the blue one'

- **Allocation:** Children referred to the number or amount of reward containers or how reward containers were allocated. Utterances with numerals (e.g., *zwei* 'two'), amounts (e.g., *alles* 'all', *viele* 'many', *keine* 'none'), and statements of allocation (e.g. *zwei für mich, zwei für dich* 'two for me, two for you') were scored.

Examples: *Ich hab schon zwei* 'I already have two'; *Alle sind raus* 'all are gone'; *Ich hab so viele* 'I have so many';

- **Fairness:** Children explicitly referred to fairness, using the words *gerecht/fair* 'fair' or *ungerecht/unfair* 'unfair'.

Example: *Sonst ist es unfair* 'Otherwise it is unfair'

- **Protest:** Children protested against the other child's behaviour (e.g., the other child taking or trying to take rewards). Utterances were only scored as protest when they included a negation ('No!') or a clear request to stop ('Don't do it!').

Examples: *Nein, ich!* 'No, me'; *Nicht meine nehmen!* 'Don't take mine!'; *Mann, nicht!* 'Man, don't!'

A fifth coder re-scored utterances from four (29%) dyads (two female and two male dyads) for reliability purposes. Agreement between coder 4 and coder 5 was excellent to good for the five coding categories (ownership: Cohen's $\kappa = 0.934$; colour: Cohen's $\kappa = 0.941$; allocation: Cohen's $\kappa = 0.708$; fairness: Cohen's $\kappa = 1$; protest: Cohen's $\kappa = 0.722$).

Data analyses. Data analyses were similar to the analyses in Study 1. As response variable, we used the number of retrieved items and not the final distribution of items. This allowed for a fairer comparison with the apes in study 1 as only human children, but not apes, occasionally transferred rewards to each other. Our full model included condition as fixed effect and the control predictors of gender, dominance, session (z-transformed to a mean of 0 and a standard deviation of 1), and trial (z-transformed). Model stability, confidence intervals and P-values of the fixed effects were calculated in the same way as in study 1. The model stability test revealed that the full model produced stable estimates. For further details, see Supplementary Information, section 2.4.

As in Study 1 we wanted to use the estimates of the intercept to test whether the proportion of own items obtained by a dyad differed from chance levels (0.5). However, the intercept optimization procedure could not be performed, because the random effects of the model were too extreme and did not allow for a reliable adjustment of the intercept. We thus calculated the average proportion of own items retrieved by each dyad per condition and tested the averages against chance using one-sample t-tests (two-tailed).

Results and discussion

Comparison of the full model to a null model (without the fixed effect of condition) revealed no significant improvement in model fit for the more complex model, $\chi^2(1) = 0.403$, $p = 0.525$. Likelihood ratio tests showed that none of the fixed effects in the full model reached significance at the 0.05 level (for details, see Table 2).

Figure 2 provides details on the proportion of own items retrieved by four-year-olds. They retrieved an average proportion of $M = 0.93$ ($SD = 0.12$) own items in the simultaneous condition and of $M = 0.94$ ($SD = 0.11$) own items in the delayed condition (see Supplementary Information, Table S7, for further details). We tested whether the proportion of own items obtained by a dyad differed from chance levels (0.5) using t-tests (for details, see Supplementary Information). In both

conditions, dyads retrieved their own food items significantly above chance (simultaneous: $t(13) = 13.45$, $p < 0.001$, $d = 3.60$, 95% CI = [0.86, 1.00]; delayed: $t(13) = 14.65$, $p < 0.001$, $d = 3.91$, 95% CI = [0.88, 1.01]). This indicates that children reliably retrieved their own rewards and refrained from taking what belonged to their partner.

The child with prior access monopolized food-containers in only 4% of trials in the delayed condition and never in the simultaneous condition (see Fig. 5). Across conditions, children wrongly retrieved one or two of their partner's items in only 32 of 224 trials (14% of trials). In 18 trials (8% of total trials), they transferred wrongly retrieved items back to their partner (see Supplementary Information, Table S5, for details).

During reward retrieval, children spontaneously referred to ownership (e.g., 'This one belongs to me', 'That one isn't yours'; simultaneous: 61% of on-topic utterances; delayed: 60%; see Supplementary Information Table S6). They occasionally referred to their assigned colours (e.g., 'You have to take the blue one') or the reward allocation ('I already have two'; see Supplementary Information Table S6). There was also occasional protest (e.g., 'Don't take mine!') in both conditions. However, children almost never explicitly mentioned fairness (simultaneous: 0% of on-topic utterances; delayed: 1%).

In summary, four-year-old human children recognized their own ownership and respected other's ownership claims following the investment of individual effort into harvesting resources. In contrast to apes, children almost never monopolized rewards in the delayed condition and, in the event they retrieved a wrong item (14% of trials), they transferred it to the correct owner more than half of the time. Importantly, children in our study referred to ownership in the majority of their on-topic utterances, but almost never referred to fairness. In addition, children in our study worked individually to harvest colour-marked resources and past work has found that young children divide resources according to work effort (Hamann, Warneken, Greenberg, & Tomasello, 2011; Kanngiesser & Warneken, 2012) and based on ownership cues like colour-markings and spatial arrangements (Ulber et al., 2015). Taken together, this suggests that

four-year-olds' retrieval of rewards was primarily driven by considerations for ownership and not by considerations for fairness. Future studies could investigate whether respect for ownership upholds when children harvest an unequal number of rewards (e.g., 1 vs. 3). Based on previous findings (Hamann et al., 2011; Kanngiesser & Warneken, 2012), we predict that German children would mostly respect what belongs to their partner in a situation of unequal reward distribution - though it is possible that children from societies with very strong norms of equal sharing would behave differently (Schäfer, Haun, & Tomasello, 2015).

Discussion

We found that captive apes failed to respect their con-specific's claim on food resources - irrespective of whether individuals had simultaneous or delayed access. In addition, apes with prior access (delayed condition) monopolized the resources in the majority of trials and left none for their partner. Human children, tested with a similar apparatus and procedure, respected their partner's claims even when they had the opportunity to maximize their own outcome in the delayed condition. Children were never explicitly told about who owned the resources, but made spontaneous verbal references to ownership during retrieval. Investment of effort into harvesting a food resource thus induced a notion of ownership and respect thereof in human children (Kanngiesser et al., 2010; Kanngiesser & Hood, 2014; Rochat et al., 2014), but not in apes. These findings highlight the uniquely cooperative nature of human ownership arrangements.

Developmental studies on respect for ownership in humans have often focused on situations, in which ownership was already established or explicitly mentioned. For example, toddlers and preschoolers settle conflicts about objects more often in favour of the owner than the non-owner (Ross, 2013; Neary & Friedman, 2014) and preschoolers are aware of their own and other's ownership rights (Blake & Harris, 2009; Kim & Kalish, 2009; Rossano et al., 2011) - even when the owner's identity is not known (Nancekivell & Friedman, 2014). There is tentative evidence that toddlers respect

claims based on more subtle cues such as colour-markings and spatial arrangements when sharing resources (Ulber et al., 2015). In line with previous work, we show that pre-schoolers recognize ownership claims based on investment of effort (Kanngiesser et al., 2010; Kanngiesser & Hood, 2014; Rochat et al., 2014) and forgo an opportunity to steal resources harvested by others to maximize their self-gain. The investment of effort appears to be a particularly strong cue to ownership (Davoodi et al., 2018; Kanngiesser et al., 2010) and is recognized by young children from diverse societies (Kanngiesser, Itakura, & Hood, 2014; Rochat et al., 2014).

Why do humans, but not other animals, have a notion of ownership? One possibility is that, on a group level, cooperative arrangements of ownership are dependent on third parties that (are willing to) punish those that disrespect others' ownership (Hume, 1739/2000). Third-party-punishment of norm transgression has been found in human adults from diverse societies (Henrich et al., 2006) and has been shown to emerge early in human ontogeny (Rossano et al., 2011; Rakoczy & Schmidt, 2013). Chimpanzees directly punish others when they are themselves victims of a transgression (i.e., second-party-punishment; Jensen, Call, & Tomasello, 2007) - to date, however, there is no conclusive evidence of third-party-punishment in apes (von Rohr et al., 2012; Riedl, Jensen, Call, & Tomasello, 2012; Schlingloff & Moore, 2018). It is possible that apes lack the social and cognitive skills (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007) to enter into and sustain cooperative ownership arrangements.

Although theoretical models of resource contests have shown that respect for ownership can emerge, in principle, in the absence of social institutions and the (threat of) punishment of ownership transgressions (Sherratt & Mesterton-Gibbons, 2015; Gintis, 2007), empirical findings often cited in support of these models are inconclusive or open to alternative explanations. (i) There is a vast literature on animal territorial contests and the advantage of prior residency (often called prior "ownership"). However, whether this advantage is based on an arbitrary convention of respect for prior residency or correlated with other, non-arbitrary factors (e.g., residents being more aggressive or larger) is debated (Kemp & Wiklund, 2004). Moreover, it has been argued

that animals' motives and intentions cannot be determined from the outcomes of fights alone (Kokko et al., 2006). In fact, if prior residency was respected, no observable fights would occur, and those fights that occurred would likely be due to intruders expecting the resident to be absent or probing the resident's fighting ability (Grafen, 1987). (ii) Different primate species have been shown to avoid taking resources that are under another's physical control or in close proximity (Kummer, 1991; Kummer & Cords, 1991; Russ et al., 2010; Sigg & Falett, 1985). Moreover, great apes show different possession-related behaviours such as defending their territories or valuing food they currently possess (Brosnan, 2011; Mitani et al., 2002; Brosnan et al., 2007; Kanngiesser et al., 2011). Importantly, none of these behaviours qualify as showing a notion of ownership because they are all dependent on physical control or constant use of the resources. Our study showed that once these factors were removed, apes failed to recognize and respect others' claims. Taken together, this casts serious doubts on claims that humans share with other animals an evolved predisposition for ownership (Sherratt & Mesterton-Gibbons, 2015; Stake, 2004; Gintis, 2007).

Given that the term "ownership" is used differently across disciplines (Tibble & Carvalho, 2018), we believe that future research would benefit from differentiating between the concept of "possession" as referring to the physical control of or close proximity to an object and "ownership" as mutually recognized and respected norms regulating how different agents relate to an object (irrespective of current possession). This would increase conceptual clarity and reduce the possibility for misunderstandings when drawing on insights from across disciplines.

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Table 1

Outputs of the reduced model predicting the proportion of own items retrieved per ape dyad in study 1. Estimates (Est) and standard errors (SE) are shown. Confidence intervals (CI_{low}/CI_{up}) were calculated via bootstraps. P-values for fixed effects were derived from likelihood ratio tests.

Parameter	Est	SE	CI_{low}	CI_{up}	χ^2	Df	P
Intercept	-0.239	0.245	-0.811	0.411	n/a	n/a	n/a
Condition ^a	-0.085	0.233	-0.670	0.511	0.128	1	0.721
Species ^b	0.538	0.249	-0.182	1.154	4.614	1	0.032
z.Session	-0.066	0.116	-0.341	0.238	0.322	1	0.571
z.Trial	-0.187	0.117	-0.484	0.129	2.502	1	0.114
Owner dominance ^c	0.134	0.239	-0.507	0.754	0.305	1	0.581
Owner sex ^d	-0.369	0.258	-1.011	0.291	2.006	1	0.157

Note. ^areference category 'delayed'; ^breference category 'bonobo';

^creference category 'sub-dominant'; ^dreference category 'female'

Table 2

Outputs of a model predicting the proportion of own items retrieved per child dyad in study 2. Estimates (Est) and standard errors (SE) are shown. Confidence intervals (CI_{low}/CI_{up}) were calculated via bootstraps. P-values for fixed effects were derived from likelihood ratio tests. Model stability is indicated by min/max values of the model estimates.

Parameter	Est	SE	CI_{low}	CI_{up}	χ^2	Df	P	Min	Max
Intercept	5.964	1.294	2.978	27.436	n/a	n/a	n/a	5.282	9.595
Condition ^a	0.351	0.557	-1.777	3.109	0.403	1	0.525	-0.334	0.767
z.Session	0.038	0.558	-1.810	1.721	0.005	1	0.946	-0.555	0.320
z.Trial	-0.298	0.236	-1.095	0.418	1.586	1	0.208	-0.408	-0.165
Owner dominance ^b	0.422	0.351	-0.931	2.699	1.468	1	0.226	0.290	0.587
Owner gender ^c	-1.359	1.422	-18.466	3.010	0.952	1	0.329	-1.994	-0.367

Note. ^areference category 'delayed'; ^breference category 'non-dominant'; ^creference category 'female'

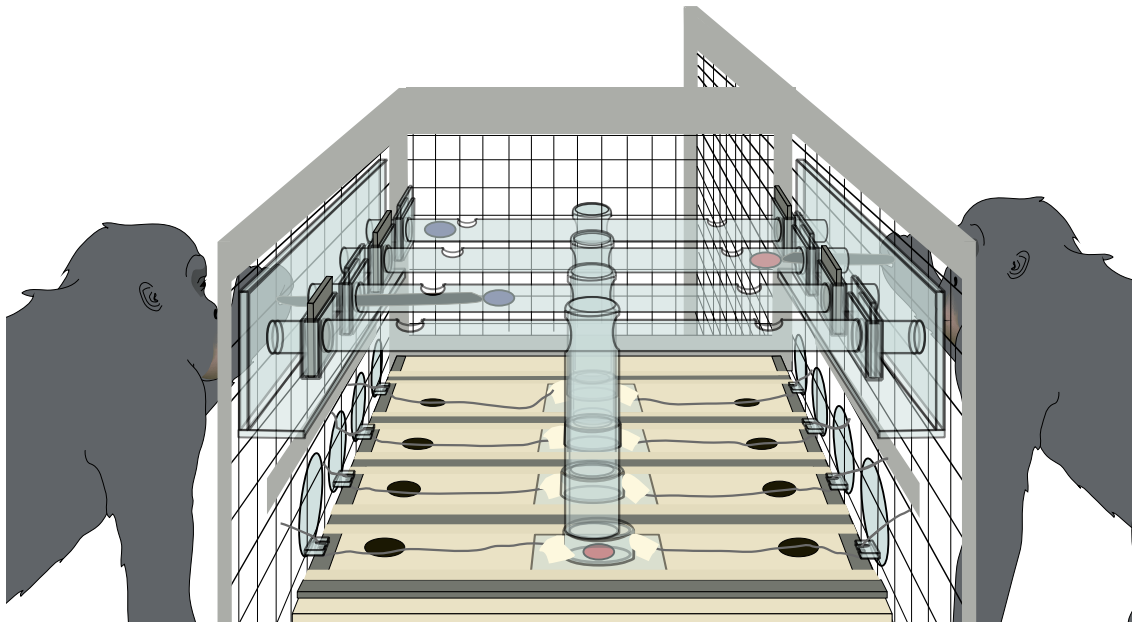


Figure 1. Experimental set-up and apparatus in Study 1. Apes were in separate rooms on each side of the apparatus. We baited the horizontal tubes with food pellets (wrapped in packing paper that was coloured with red or blue food dye). Apes had to harvest food items by pushing them to the middle of the tube where they dropped onto sliding trays. Access to the trays was blocked until the experimenters removed both grey barriers (simultaneous condition) or one gray barrier (delayed condition).

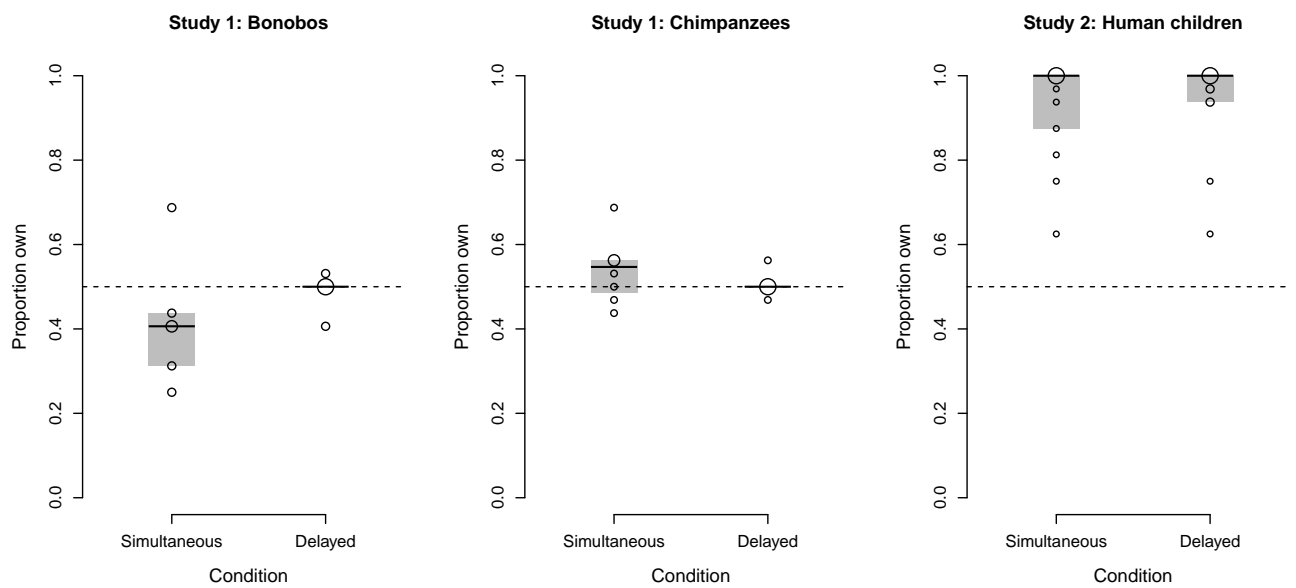


Figure 2. The average proportion of own items ($N_{own.items}/N_{retrieved.items}$) retrieved per dyad in each condition in Study 1 (bonobos, chimpanzees) and Study 2 (human four-year-olds). The area of the circles represents the number of dyads (range: 1-8) that retrieved the indicated average proportion. Solid black lines represent medians and grey boxes the second and third quartile. Dotted lines represent chance level (0.5).

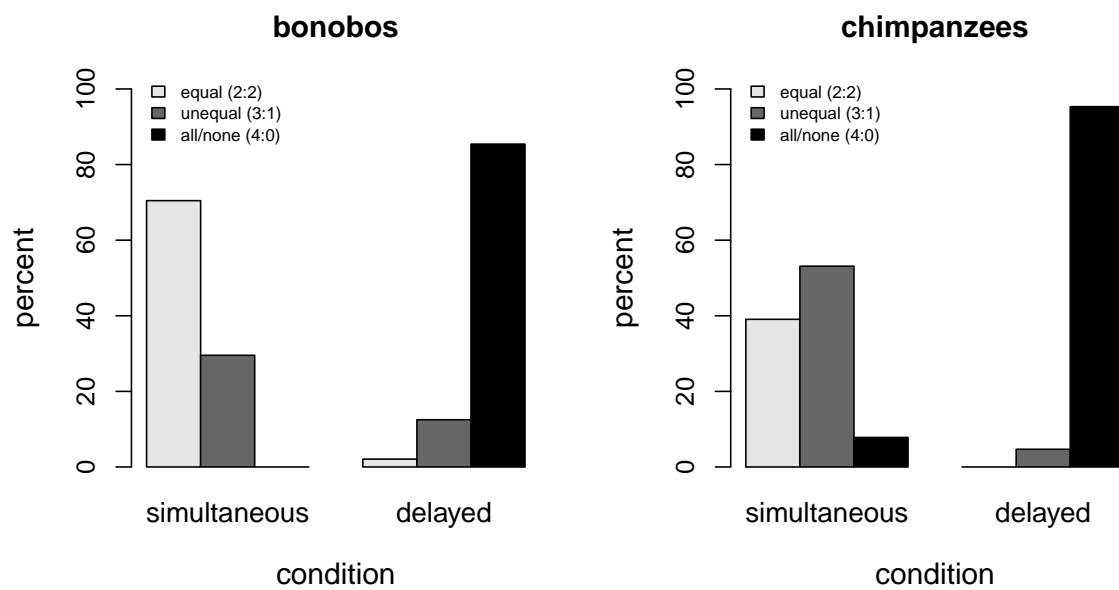


Figure 3. Percentage of trials with equal, unequal or all/none reward distribution (irrespective of ownership) in Study 1. Light grey bars indicate equal distribution (i.e., each individual retrieved two rewards), dark grey bars indicate unequal distribution (i.e., one individual retrieved three rewards, the other individual one reward), and black bars indicate all/none distribution (i.e., one individual retrieved all four rewards).

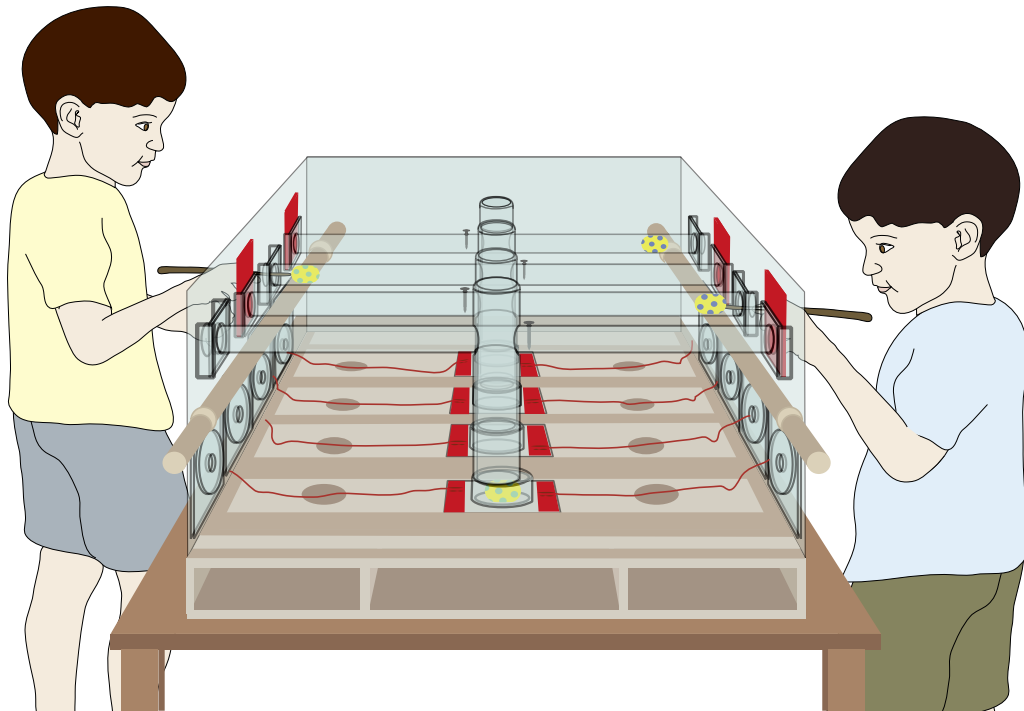


Figure 4. Experimental set-up and apparatus in study 2. Children were in the same room on separate sides of the apparatus. We baited horizontal tubes with small containers containing gummy bears. Children had to harvest the food by pushing the containers to the middle of the tube to drop them onto sliding trays. Access to the trays was blocked until the experimenter turned the wooden rods.

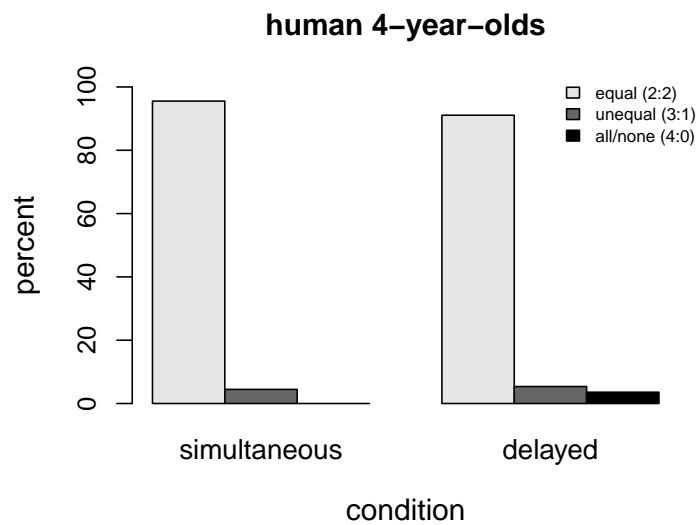


Figure 5. Percentage of trials with equal, unequal or all/none reward distribution (irrespective of ownership) in Study 2. Data for retrieved rewards was used (and not the final distribution) to ensure comparability to the ape data. Light grey bars indicate equal distribution (i.e., each individual retrieved two rewards), dark grey bars indicate unequal distribution (i.e., one individual retrieved three rewards, the other individual one reward), and black bars indicate all/none distribution (i.e., one individual retrieved all four rewards).