Reciprocal Altruism and Bartering Capacities in Monkeys and Great Apes

by Marie Pelé Ph.D.

Trading is a hallmark of human behavior. Exchanges or even gifts are not commonly seen in other species and humans appear as the only species having developed efficient economic strategies. However, little is known about the evolutionary origin of human trading capacities. Across the animal kingdom, reciprocal interactions are reported in a diversity of contexts such as social grooming, coalitions and food sharing. In primates, however, cooperation is mostly constrained by social factors such as affiliation and hierarchy between group members. Individuals often interact more with kin than non-kin and, in species of low social tolerance, favors are mainly given to members of one's own kin subgroup. In humans the use of money has overcome these kinds of constraints by normalizing exchanges between individuals regardless of clans, groups or cultures. Normalized bartering has only recently spread in human beings, beginning in historical time. Prior to conventional exchanges, Hominoid bartering was probably partially restrained by social constraints like those found in non-human primates.

Based on mental scorekeeping of given and received favors, calculated reciprocity would approach the economic computations performed by humans. Many examples of reciprocation between two conspecifics have been described among primates. Nonetheless, reported instances of reciprocity based on an exact calculation of what has been given and what has been received remain anecdotal. The lack of evidence for calculated reciprocity in nature has led to a reappraisal of its cognitive prerequisites. It implies capacities like estimating the values of goods, memorizing what is given and received, accepting a loss, anticipating a return or controlling the partner's behavior. While it is difficult to appreciate the expectations of an animal about to give a service to another in the social context, experimental studies can investigate the goals of an individual who gives an object.

My work aimed at studying the conditions necessary for calculated reciprocity to occur (1) by testing whether primates understand the temporal cost associated with an exchange, (2) by studying the capacity of primates to take a risk during an exchange and (3) by searching whether primates are capable to engage with a conspecific in a calculated exchange under controlled conditions. I tested seven species of non human primates in different exchange tasks: long-tailed macaques (*Macaca fascicularis*), Tonkean macaques (*M. Tonkeana*), capuchin monkeys (*Cebus apella*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orangutans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla*). The benefit brought by such task is that it only requires the animals to perform a single simplistic gesture, i.e. giving something, which requires minimum training contrary to most tool-using tasks. In addition, giving is a behavior that is naturally present in various primate species such as apes, capuchins or macaques.

During a postponed exchange, the first donor needs to accept the delay between the decision to cooperate and the return of the favor by the partner. In a first experiment, I involved capuchins, macaques and chimpanzees in four delay-of-gratification tasks to assess their abilities to sustain a delay. Subjects were required to wait for increasing time delays before exchanging a small edible item for a larger one with a human partner. When considering this temporal dimension of exchange, I observed some variations in the capacity of primates to delay gratification. For a reward equivalent to eight times an initial item, capuchins could wait for 10-20 s [1], macaques for 40-80 s [1,2] and chimpanzees for 1-2 min [3]. In all species, both estimation of the value of goods being exchanged and anticipation of the waiting duration underlie the decision of individuals.

During a delayed exchange, animals must also be capable to estimate variable payoffs. In a second experiment, I investigated whether capuchins, macaques and orangutans estimate the chances of different outcomes. In a food-gambling game, I gave subjects the opportunity to gamble a piece of cookie with a human experimenter for pieces of larger, equal or smaller sizes. The chances of losing or gaining were manipulated *via* different combinations of rewards presented in 6 aligned plastic cups. While individuals can estimate the probability to receive a valuable reward, they have no possibility to accurately predict what they will receive. They therefore have to decide whether to risk the item already in their possession based on the probability of receiving a better payoff. Results highlighted an unexpected ability to engage in gambling in most individuals for all three species. Gambling decisions were negatively induced by the probability of losing and positively by previous outcomes. When confronting data to economic decision-making in humans, it appeared that non-human primates evaluate gambles in terms of deviations to a reference outcome, i.e. cumulative prospect theory [4].

Thus, primates are capable to sustain important delays and to estimate loss probabilities. They appear capable to consider when deciding to engage or not in an exchange. Though we know that two individuals may reciprocate, the ability of primates to directly exchange goods has not been systematically tested. In a dyadic context where subjects optimize their gain by bartering tokens, I expected that great apes will exchange more readily than monkeys. I have tested chimpanzees, bonobos, gorillas, orangutans, Tonkean macaques and brown capuchins in a token-exchange task involving two conspecifics and a human experimenter. Tested by pairs, subjects had to exchange token with partner to obtain food from the experimenter. I observed 4, 5, 264 and 328 transfers of tokens in gorillas, chimpanzees, orangutans and bonobos, respectively. Most gifts were indirect in gorillas, chimpanzees and bonobos, whereas most were direct in orangutans. Contrary to orangutans, only few begging gestures and gifts were observed in chimpanzees, bonobos and gorillas; and individuals were not capable to reciprocate [5]. In capuchins and macaques, no begging gesture nor gifts has been observed [6]. However, by increasing the number of sessions, two orangutans – a male and a female - were able to engage in a system of exchanges that was both stable and calculated. Although initially the transfers were biased in one direction, they became more balanced towards the end of the study. I observed an increase in the number and complexity of exchanges and alternations. This study is the first experimental demonstration of the occurrence of direct transfers of goods based on calculated reciprocity in non-human-primates [7].

Although spontaneous exchange is difficult in non-human primates, this work shows that they possess some abilities to evaluate the value of goods, to accept a loss and to delay gratification, which are among the required capacities underlying economics transactions as observed in human beings.

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Token Transfers Among Great Apes (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan paniscus*, and *Pan troglodytes*): Species Differences, Gestural Requests, and Reciprocal Exchange

Marie Pelé
Université de Strasbourg

Valérie Dufour
University of St. Andrews

Bernard Thierry
Université de Strasbourg

Josep Call
Max Planck Institute for Evolutionary Anthropology

Great apes appear to be the nonhuman primates most capable of recognizing trading opportunities and engaging in transfers of commodities with conspecifics. Spontaneous exchange of goods between them has not yet been reported. We tested gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*), bonobos (*Pan paniscus*), and chimpanzees (*Pan troglodytes*) in a token-exchange task involving two conspecifics and a human experimenter. Tested in pairs, subjects had to exchange tokens with a partner to obtain food from the experimenter. We observed 4, 5, 264, and 328 transfers of tokens in gorillas, chimpanzees, orangutans, and bonobos, respectively. Most gifts were indirect in gorillas, chimpanzees, and bonobos, whereas most were direct in orangutans. The analysis showed no evidence of calculated reciprocity in interactions. A main finding of the study was the high rate of repeated gifts and begging gestures recorded in orangutans. This raises the question of the meaning of pointing in great apes and their ability to understand the communicative intent of others.

Keywords: reciprocity, exchange, tokens, begging, great apes

Animals engage in reciprocal interactions, but they do not commonly exchange goods or services like humans do. On the basis of mental scorekeeping of given and received favors (de Waal & Lutrell, 1988), calculated reciprocity would approach the economic computations performed by humans. Several authors have assumed that calculated reciprocity accounts for exchanges of commodities in chimpanzees (*Pan troglodytes*); for example, males groom females to increase their chances of mating, or they share meat according to the amount of help provided in hunting (de Waal, 1989; Mitani & Watts, 2001). Finding correlations between given and received actions, however, is not sufficient to demonstrate that chimpanzees take into account the costs and benefits of reciprocated behaviors (Hemelrijk, 1996). Measuring the extent to which apes exchange commodities on the basis of calculation is a tricky issue, and any correspondence between gifts and returns must be considered with caution (Seyfarth & Cheney, 1988). Benefits exchanged by individuals may vary in nature from one individual to another and from one occasion to the next. In addition, the same currency may have a relative value depending on individuals, value that would be based on factors such as age, size, and dominance status.

Although it is difficult to appreciate the expectations of an individual who gives a service to another in the social context, experimental studies allow one to control for the value of goods about to be exchanged. Studies of chimpanzees and brown capuchin monkeys have demonstrated that they readily engage in exchanges with human experimenters, creating situations in which one may examine the cognitive abilities necessary for trading. They give food to receive another food that is quantitatively or qualitatively more desirable (Drapier, Chauvin, Dufour, Uhlrich, & Thierry, 2005; Lefebvre, 1982; Lefebvre & Hewitt, 1986; Padoa-Schioppa, Jandolo, & Visalberghi, 2006). They exchange nonedible tokens for food with an experimenter (Brosnan & de Waal, 2005; Hyatt & Hopkins, 1998; Westergaard, Liv, Chavanne, & Suomi, 1997; Westergaard, Liv, Rocca, Cleveland, & Suomi, 2004). They learn the use of tokens from conspecifics (Brosnan & de Waal, 2004; Sousa, Okamoto, & Matsuzawa, 2003); chimpanzees even stock the tokens needed to obtain rewards (Sousa & Matsuzawa, 2001), and capuchin monkeys use tokens as symbols

Marie Pelé and Bernard Thierry, Département Ecologie, Physiologie, and Ethologie, Institut Pluridisciplinaire Hubert Curien, Centre National pour la Recherche Scientifique, Université de Strasbourg, Strasbourg, France; Valérie Dufour, School of Psychology, University of St. Andrews, St. Andrews, Scotland; Josep Call, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

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Correspondence concerning this article should be addressed to Marie Pelé, Département Ecologie, Physiologie, and Ethologie, UMR 7178, Institut Pluridisciplinaire Hubert Curien, Centre National pour la Recherche Scientifique, 23 rue Becquerel, 67087 Strasbourg Cedex 2, France. E-mail: marie.pele@c-strasbourg.fr

to represent and combine quantities (Addessi, Crescimbene, & Visalberghi, 2007, 2008). The use of tokens makes it possible for experimenters to normalize exchange parameters and to control differences of currencies or the relative values of the goods to be exchanged.

Although numerous studies have shown that primates may exchange with a human experimenter, observations of active transfers between conspecifics remain scarce (de Waal, 1989, 1997). In de Waal's (1997) study, most food transfers recorded in capuchins were passive; food was collected by an individual through a separating mesh after having been dropped by the initial possessor. Active transfers included both indirect transfers—that is, the possessor dropped the item in the partner's cage—and direct transfers—that is, the possessor transferred an item directly to the partner's mouth or hand (de Waal, 1997; de Waal, Luttrell, & Canfield, 1993). Only active transfers might involve intentionality to give, and they were rarely observed (de Waal, 1997; de Waal et al., 1993). In the Westergaard and Suomi (1997) study, capuchins were able to solve a cooperative task by transferring stones through a mesh in an active and indirect way. A similar instance of indirect transfer of a tool was previously reported in a captive hamadryas baboon (*Papio hamadryas*; Beck, 1973). A single case of direct transfers of a tool from one individual to another was observed in chimpanzees. Two young males trained in a symbol language proved being able to ask one another for an appropriate tool needed to obtain food. Once the reward was obtained, it was shared between the individuals, who were also able to reverse their roles of tool requester and food provider (Savage-Rumbaugh, Rumbaugh, & Boysen, 1978). A recent attempt to replicate this study in capuchin monkeys showed that direct gifts of a tool may occur in subjects trained to exchange, but the donor never received a share of the reward (Westergaard, Evans, & Howell, 2007). Until now, no experimental study has addressed the conditions needed for direct transfer of goods to occur among nonhuman primates.

Given their social and cognitive skills, great apes stand as the nonhuman primates most likely to be capable of recognizing potential trading opportunities and to engage in direct transfers with conspecifics. They may notably collaborate with a conspecific partner (chimpanzees, Melis, Hare, & Tomasello, 2006a, 2006b), and recent findings have suggested that they can plan for the future (bonobos and orangutans, Mulcahy & Call, 2006; chimpanzees, Dufour, & Sterck, 2008). To assess great apes' trading capacities, we tested gorillas, orangutans, bonobos, and chimpanzees in a triadic token-exchange task involving two conspecifics and a human experimenter. Each individual had three types of tokens at her or his disposal: self-valued tokens exchangeable for food with the human experimenter, partner-valued tokens that the partner could exchange for food with the human experimenter, and no-value tokens that could not be exchanged. This meant that subjects could exchange their self-valued tokens with the experimenter for food. Additionally, subjects had the option of exchanging their partner-valued tokens with each other and then exchanging the new self-valued token with the experimenter for food. Given their abilities to cooperate with a conspecific (Melis et al., 2006a, 2006b), we expected that chimpanzees and bonobos would show better results than gorillas and orangutans in such task.

Method

Subjects

Subjects were 3 gorillas (*Gorilla gorilla*), 5 orangutans (*Pongo pygmaeus*), 5 bonobos (*Pan paniscus*), and 4 chimpanzees (*Pan troglodytes*) housed at the Wolfgang Köhler Primate Research Center, Leipzig Zoo (Leipzig, Germany). Table 1 presents their age, sex, and rearing history. All subjects were socially housed in enclosures with access to indoor and outdoor areas and sleeping rooms for the night. Water was available ad libitum, and subjects were not food deprived at any time. Before this study, they had been involved in various cognitive tasks, but none involved exchanging objects.

Table 1
Self-Value Tokens and Age, Sex, and Rearing History of Subjects

Name	Species	Age (years)	Sex	Rearing history	Self-value token: Set 1	Self-value token: Set 2
Joe	Bonobo	23	Male	Nursery	Green PVC tube	Gray PVC triangle
Lim	Bonobo	11	Male	Nursery	Green PVC tube	Transparent PVC circle
Kun	Bonobo	10	Male	Nursery	Gray PVC cube	L-shaped metallic
Uli	Bonobo	13	Female	Mother	Green PVC tube	L-shaped metallic
Yas	Bonobo	9	Female	Mother	Gray PVC cube	Transparent PVC circle
Bim	Orangutan	26	Male	Mother	Gray PVC cube	L-shaped metallic
Dun	Orangutan	33	Female	Unknown	Gray PVC cube	Gray PVC triangle
Pin	Orangutan	18	Female	Mother	Green PVC tube	L-shaped metallic
Dok	Orangutan	15	Female	Mother	Green PVC tube	Transparent PVC circle
Pad	Orangutan	9	Female	Mother	Gray PVC cube	Transparent PVC circle
N'Di	Gorilla	29	Female	Unknown	Gray PVC cube	No retraining
Beb	Gorilla	27	Female	Unknown	Green PVC tube	L-shaped metallic
Vir	Gorilla	11	Female	Mother	Green PVC tube	Transparent PVC circle
Uny	Chimpanzee	9	Male	Mother	Gray PVC cube	Transparent PVC circle
Jah	Chimpanzee	13	Female	Mother	Gray PVC cube	L-shaped metallic
Ger	Chimpanzee	13	Female	Mother	Green PVC tube	L-shaped metallic
Fif	Chimpanzee	13	Female	Mother	Green PVC tube	Transparent PVC circle

Note. PVC = polyvinyl chloride.

Tokens

Tokens differed in form and color, and some could be exchanged for food in the experiment. Tokens used were 5-cm-long green polyvinyl chloride (PVC) tubes, a gray PVC cube with 5 cm × 5 cm sides, 5-cm-long metallic chain links, a 5-cm-long L-shaped metallic token, a 5 cm × 5 cm × 5 cm gray PVC triangle, and a 5-cm-diameter transparent PVC circle (see Figure 1).

We gave 2 subjects the same set of 36 tokens, consisting of three types of 12 tokens: (a) *Self-valued tokens* were valuable to the subject and valueless to the partner, (b) *partner-valued tokens* were valuable to the partner and valueless to the subject, and (c) *no-value tokens* were not valuable to any animal. Table 1 gives information about each subject's self-value tokens.

Training Procedure

We trained subjects individually to exchange one of three types of tokens for food in a testing room of 25 m^2. Before each training session, we placed the set of 36 tokens in a compartment of the testing room. The experimenter (Marie Pelé) sat in front of the compartment close to the 36 tokens, and the subject entered in the testing room. Subject and experimenter could give and receive tokens through a mesh panel (68 × 48 cm). The tokens had to fit into a 5-cm × 5-cm square and required some effort to be inserted through the mesh. A session typically started with the experimenter requesting tokens by holding an open hand (palm up) next to the fence. To inform the subject that she or he had to select the token to be given (the self-valued token), only one kind of token (e.g., gray cube) was rewarded with a grape or a piece of banana (depending on species). Any correct token was placed in a bowl, whereas an incorrect token (i.e., one with no value for the subject, i.e., partner-valued or no-value tokens) was thrown into a bucket without being rewarded. Once the subject had returned his or her 12 self-valued tokens, the experimenter left the testing room for 3 min. Then the experimenter came back, stayed for 3 min, and then left the room, which ended the session. If during the 3 min the subject gave the remaining incorrect tokens, the experimenter collected them and dropped them in the bucket without rewarding the subject.

Testing started once subjects succeeded in giving more than 90% of the correct tokens first, during three consecutive sessions. Because the dominant gorilla male showed no interest in the task, he was not trained further. All other subjects reached the criterion.

Testing Procedure

Testing took place in the same testing room divided into two testing compartments by a common mesh wall through which subjects could interact and transfer tokens with each other (see Figure 2). The experimenter sat in a rectangular booth facing both testing compartments. The booth had a front window (98 × 95 cm) and two mesh panels (68 × 48 cm) on either side and allowed the apes to look at each other.

We placed the same set of 36 tokens (12 self-valued tokens for subject, 12 partner-valued tokens, and 12 no-value tokens) in each compartment, near the experimenter exchange area and opposite the common mesh wall (see Figure 2). The experimenter resumed a sitting position in the booth, and subjects were let in.

The testing procedure was the same as the training one except that 2 individuals were present in each of two adjacent compartments. In the first part of a session, partners had the possibility of exchanging their self-valued tokens with the experimenter. Once both individuals had given all their 12 self-valued tokens, the experimenter left the room for 3 min to not influence possible transfers between subjects. In the subjects' compartments, only partner-valued and no-value tokens remained. After 3 min elapsed, the experimenter came back and sat with the subjects for a minimum duration of 3 min. If a transfer of a valuable token had occurred, the experimenter asked the subject for the token and exchanged it for food. If a transfer of tokens occurred after the experimenter came back, she also asked the relevant subject for the token and stayed in the testing room until extinction of transfers of any kind. Four cameras recorded subject behavior during the session, and a second observer collected latencies of exchanges with the experimenter.

Twelve trials were run for each pair of individuals. One exception was a pair of chimpanzees (Uny and Jah) for whom only 10 trials were conducted because of some difficulties in selecting the

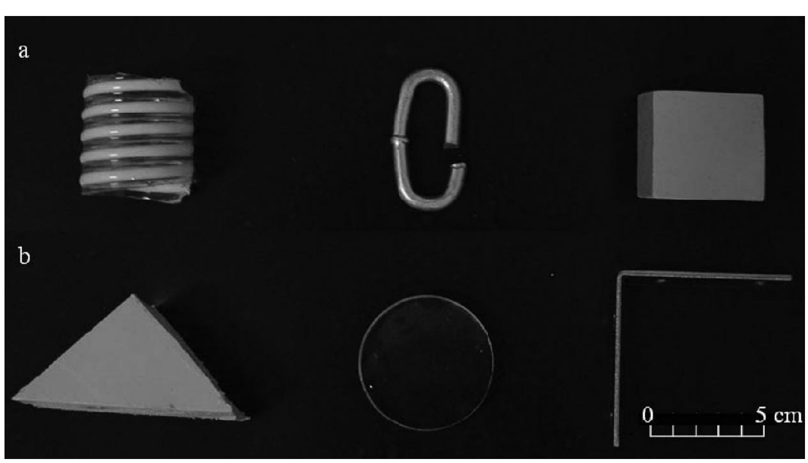

Figure 1. Sets of tokens: (a) Set 1: green polyvinyl chloride (PVC) tube, metallic chain, and gray PVC cube and (b) Set 2: gray PVC triangle, transparent PVC circle, and L-shaped metallic token.

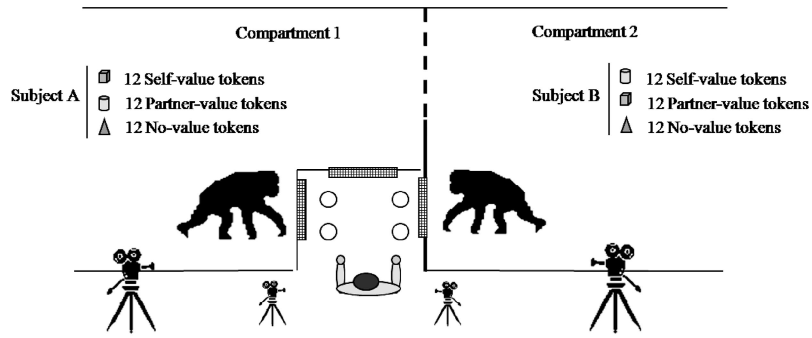

Figure 2. Experimental setting: Two partners, Subjects A and B, receive the same set of tokens: 12 self-valuable tokens, 12 partner-valuable tokens, and 12 no-value tokens. Tokens were placed near the panel mesh of the booth, out of the partner's reach. The common mesh wall (dashed line) is situated at the bottom of the testing room. Tokens could be transferred by passing them through the common mesh or the space existing between the floor and the wall separating the two compartments.

individuals. For each species, we tested all possible pairs of individuals. The number of subjects allowed us to test three pairs of gorillas (24 sessions per individual), 10 pairs of orangutans and bonobos (48 sessions per individual), and six pairs of chimpanzees (36 sessions for Ger and Fif; only 34 sessions for Uny and Jah). Because some individuals shared the same self-valued tokens, they could not be tested together with the original set of tokens. Therefore, training and testing phases were run again with a new set of tokens (see Figure 1).

Video Processing

Test sessions were scored from videotapes using behavioral observation software (The Observer [Noldus Corporation, Leesburg, Virginia] and Interact [Mangold Corporation, Atlanta, Georgia]). The behavioral units recorded during testing sessions were (a) *exchange with experimenter* (a subject passes a token through the mesh to the experimenter); (b) *transfer with partner* (a subject obtains a token that was originally in her or his partner's compartment; (c) *pointing* (a subject puts its fingers through the mesh separating both compartments in the direction of one or more tokens); and (d) *holding out hand* (a subject holds one hand with the palm up in the partner's direction). We recorded the frequency and latency of the first two behaviors as well as the tokens' value. The second two behaviors were the only begging gestures observed during the testing period in all species. We recorded both their frequency and the identities of actor and recipient.

Five different types of transfers were observed during test sessions. In *catch*, the subject places tokens near the common mesh by manipulating or playing with it. The partner takes one token in the subject's compartment. The subject attempts to prevent it or does not see it. In *passive transfer*, a subject brings a token near the common mesh wall and lets the partner take it. In *indirect gift*, a donor places a token in the partner's compartment without physical contact with the partner. In *direct gift*, a subject gives a token to the partner by passing it through the common mesh or under the common wall; transfers occur directly from hand to hand, hand to mouth, mouth to hand, or mouth to mouth. Contrary to indirect gifts, one may safely assume that direct gifts involve an intention to give. For *unknown*, the type of transfer is unknown because it was not clearly visible on the cameras; this might have been the case when the experimenter left the testing room.

Assessment of Social Relationships

Individuals were observed in their social groups to assess the quality of social relationships between subjects. Observational data were collected during the testing period of each group. The observer (Marie Pelé) conducted observations from a platform above the inside enclosures of 264 m^2, 230 m^2, and 175 m^2 for gorillas, orangutans, and chimpanzees, respectively, and the outside enclosure of 2,300 m^2 for bonobos. All members of each species (including juveniles) were observed 1.5 hr per day between 9:00 a.m. and 5:00 p.m., totaling 60 hr for gorillas, 50 hr for orangutans, 34 hr for bonobos, and 60 hr for chimpanzees. Every 5 min, the observer recorded distances between group members ($<$1 m and physical contact), their locations in the enclosure, and their individual activities—rest, locomotion, feed, play, allogroom, or self-groom—using the scan-sampling method (Altmann, 1974). Seven hundred fifty-three scans per individual were recorded for gorillas, 626 per individual for orangutans, 420 per individual for bonobos, and 760 per individual for chimpanzees.

Statistical Analyses

We used several nonparametric statistics: Kruskal-Wallis test to compare frequencies of transfers and begging gestures between species followed by a Dunn's multiple pairwise comparison for each mean comparison, Wilcoxon's matched-pairs test (one-tailed) to compare the frequencies of the different types of transfers, and Fisher's exact test to compare the percentages of the different types of transfers (Siegel & Castellan, 1988). For each trial, we used data from only 1 subject that we chose by randomization. Thus, for one pair of individuals, we considered data of a subject for six trials and data of his or her partner for the other six trials. In addition, given the small number of individuals of each species, we used an exact test procedure to carry out nonparametric analyses (SPSS 16 [SPSS Inc., Chicago] and GraphPad Prism 5 GraphPad Software, Inc., La Jolla, CA).

To test for reciprocity, frequencies and latencies of behaviors scored were analyzed using matrices. For each behavior, we generated initiator and receiver matrices to compare the amount of behavior given with the amount of behavior received. Matrix correlations were tested using Dietz's test, based on 10,000 permutations (Matman software; de Vries, Netto, & Hanegraaf, 1993).

For all analyses, we fixed the significance level at .05. Average values are given as means ± standard errors of the mean.

Results

Training Phase

To reach the criterion in the discrimination of the self-valued token, apes needed an average of 5.8 ± 0.5 sessions for the first set of tokens and 5.1 ± 0.6 sessions for the second set of tokens (see Figure 3). Speed of learning acquisition for the first set of tokens differed significantly between species, Kruskal-Wallis test: $\chi^2(3) = 8.037$, $p = .027$. Gorillas needed more training sessions than chimpanzees (Dunn's multiple comparison test, $p < .001$; see Figure 3). Speed of acquisition for the second set of tokens did not differ significantly between species, Kruskal-Wallis test: $\chi^2(3) = 1.390$, $p = .736$.

Exchange With the Experimenter

Each testing session started with individuals exchanging their 12 self-value tokens with the human experimenter. The 12 tokens first given by the subject were composed of more than 90% of self-valued tokens for all individuals of all species. The totality of self-valued tokens was exchanged in a mean of 3.83 ± 0.09 min (gorillas, $M = 4.73 \pm 0.31$ min; orangutans, $M = 3.77 \pm 0.14$ min; bonobos, $M = 3.97 \pm 0.18$ min; chimpanzees, $M = 3.23 \pm 0.12$ min).

Transfers of Tokens Between Subjects

The total number of transfers for each species, including catches, passive transfers, and indirect and direct gifts, was 4 for gorillas (0.11 transfer per session), 264 for orangutans (2.20 transfers per session), 328 for bonobos (2.73 transfers per session), and 5 for chimpanzees (0.07 transfers per session; see Figure 4). We discarded those cases in which an individual put a token in the partner's cage and then took it back (61 cases with a female bonobo, Yas; see next section). We also excluded transfers involving infants (gorillas, 12 transfers; orangutans, 37 transfers) from the analysis.

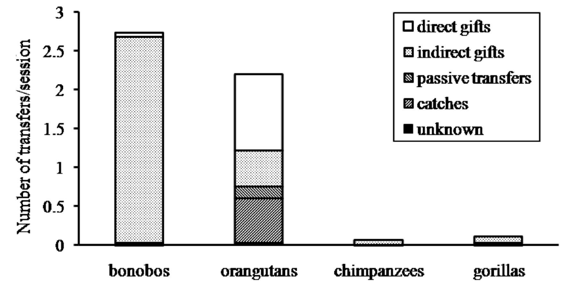

Figure 4. Number of transfers per session for all species.

Orangutans displayed the greatest variety of transfer types, including gifts (67% of the total), catches (26%) and passive transfers (7%). Most of the transfers observed in the other species were represented by gifts (bonobos, 97%; chimpanzees, 80%; and gorillas, 75%). Because gifts accounted for most of the observed transfers in all species, in the following sections we compare the species on frequency of direct and indirect gifts (see Figure 5). Species differed significantly in the frequency of direct gifts, Kruskal-Wallis test: $\chi^2(3) = 9.744$, $p = .011$. In contrast, species did not differ significantly in the frequency of indirect gifts, Kruskal-Wallis test: $\chi^2(3) = 1.772$, $p = .649$.

Value of Tokens Transferred

We analyzed whether the donor preferentially transferred those tokens that were valuable to the partner as opposed to those that were not. Overall, donors did not preferentially transfer tokens that were valuable to the partner in direct gifts (Wilcoxon's test: $z = -1.51$, $p = .125$, $N = 5$, one-tailed, $M_1 = 9.8 \pm 3$, $M_2 = 6 \pm 1.9$) or indirect gifts (Wilcoxon's test: $z = -0.14$, $p = .460$, $N = 8$, one-tailed, $M_1 = 12.2 \pm 10.5$, $M_2 = 5.3 \pm 2.4$). However, there were large individual differences in both the number of tokens transferred and the preference for partner-valued tokens. Table 2 lists those individuals that produced five or more gifts. With regard to direct gifts, 2 orangutans preferentially transferred partner-valued tokens, whereas another orangutan preferentially trans-

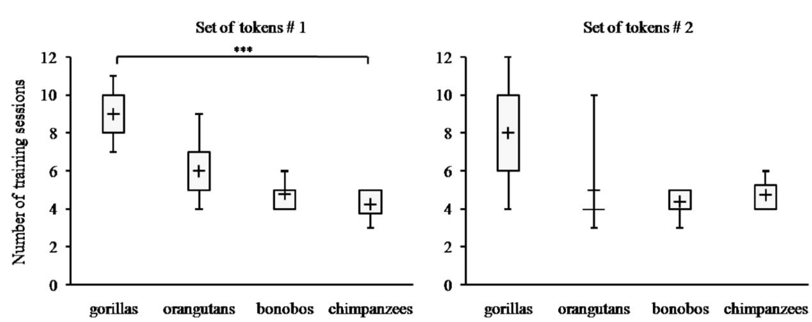

Figure 3. Number of training sessions needed to reach the criterion for all species with the first set of tokens (left panel) and the second set of tokens (right panel). Boxplots represent the interquartile range with minimum and maximum, and black plus signs indicate means. (Dunn's post hoc $p < .001$).

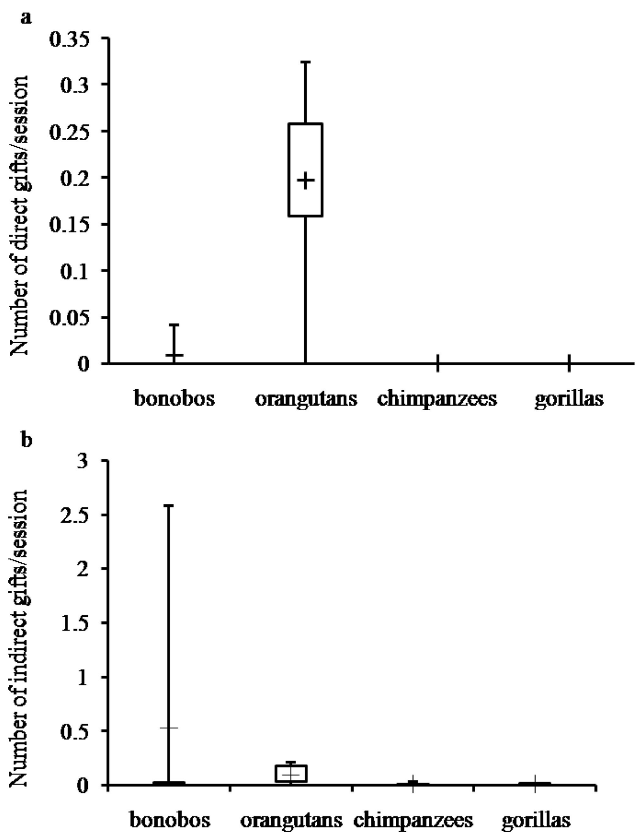

Figure 5. Number of direct gifts per session (a) and number of indirect gifts per session (b) for all species. Boxplots represent the interquartile range with minimum and maximum, and black plus signs indicate means.

ferred no-value tokens. With regard to indirect gifts, 1 bonobo preferentially transferred partner-valued tokens, whereas an orangutan preferentially transferred no-value tokens.

The behavior of this bonobo appeared to be a consequence of her inclination to play with one of the tokens (i.e., green tube) by inserting it through the fence into her partner's cage and attempting to take it back afterward, which she did successfully 61 times. In the remaining cases, the tokens were seized by the partner, who exchanged them for food with the human experimenter. This behavior decreased dramatically (from 7.7 transfers per session to 0.25) with the introduction of the L-shaped metallic token from the second set of tokens.

Gestures: Pointing and Hand Begging

Figure 6 illustrates the occurrence of pointing and hand begging per testing session for all individuals in the four species. Orangutans performed communicative behaviors more often than other species. There were significant differences across species in the frequency of hand begging, Kruskal-Wallis test: $\chi^2(3) = 15.425$, $p < .001$. A Dunn's multiple comparison test showed that orangutans produced significantly more holding-out-hand behavior than each of the three other species ($p < .05$ for each). In contrast, there were no significant differences between species in the frequency of pointing, Kruskal-Wallis test: $\chi^2(3) = 2.400$, $p = 1$. Because the frequency of these behaviors was so low for other species, the next analyses focused exclusively on orangutans. Holding out the hand led to a direct gift from the partner 28.1% of the time and to an indirect gift 7.8% of the time. Pointing led to a direct gift from the partner 17.4% of the times and to an indirect gift 15.2% of the time.

To assess the efficiency of these two behaviors in term of token values, we checked whether an individual received self-valued or no-value tokens after using such gestures. When followed by gifts, 80% (12 cases) of pointing behaviors were followed by gifts of valuable tokens and 20% (three cases) by gifts of no-value tokens. Considering holding-out-hand behavior, we observed that this gesture was followed an equal number of times by gifts of valuable tokens (23 cases) and gifts of no-value tokens (23 cases). We checked whether the number of these two behaviors followed by valuable gifts or by no-value gifts differed significantly from chance. For the subject who produced most begging gestures (Bim for both), we compared the observed probability of self-valuable tokens he received after begging with the chance level calculated for each event in function of the number of valuable tokens and no-value tokens available to the partner. After holding out his hand, Bim did not receive more self-valued tokens than expected by chance (Wilcoxon's test: $z = -0.33$, $p = .372$, $N = 34$, one-tailed, $M_1 = 0.50 \pm 0.01$, $M_2 = 0.44 \pm 0.08$). By contrast, after pointing Bim received more self-valued tokens than expected by chance (Wilcoxon's test: $z = -3.09$, $p < .001$, $N = 14$, one-tailed, $M_1 = 0.45 \pm 0.01$, $M_2 = 0.85 \pm 0.09$).

Reciprocity in Orangutans?

Despite the elevated number of direct gifts observed in orangutans, we did not find a statistically significant correlation between the matrices of the total number of tokens given and received by subjects, nor did we find one for indirect gifts (Dietz's test; $p =$

Table 2
Percentage of Direct and Indirect Gifts in Which the Donor Transferred Tokens That Were Valuable to Her Partner

		Direct			Indirect		
Name	Species	%	*N*	*p*	%	*N*	*p*
Bim	Orangutan	78.9	19	<.0001	50	4	—
Pin	Orangutan	74.4	39	<.0001	83.3	6	<.0001
Dok	Orangutan	62.1	29	.116	60.0	25	.200
Pad	Orangutan	29.0	31	.003	4.8	21	<.0001
Yas	Bonobo	60.0	5	.200	89.6	309	<.0001

Note. Only those subjects with five or more gifts are displayed (Fisher exact test).

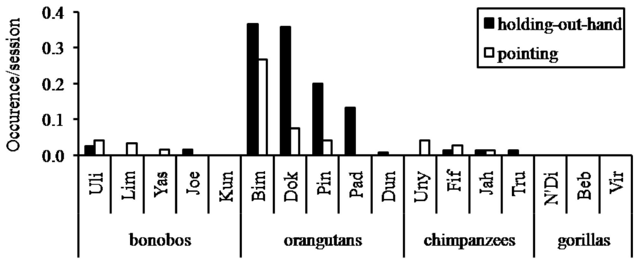

Figure 6. Occurrence per session of holding out the hand and pointing behaviors recorded for all individuals of the four species.

.233, rs = .21) or direct gifts (Dietz's test; p = .146, rs = .56), regardless of the value of tokens transferred. Still, in the 120 sessions conducted for this species, we recorded one likely instance of reciprocal transfers between 2 orangutans in the course of one session. We observed 2 orangutans, 1 male (Bim) and 1 female (Dok), exchanging partner-valued tokens with each other during the seventh session. Transfers occurred in the experimenter's presence. First, the female gave directly to the male a cube that was his valued token. After exchanging this cube with the experimenter for a piece of banana, the male took some tubes and metallic chain links and pushed one tube under the common mesh wall. The female took it and exchanged it with the experimenter for the food reward. Then, the male took a cube that had been placed by the female near the common wall and exchanged it with the experimenter. At this moment, the female grabbed five tubes in the partner's compartment out of his sight. After having exchanged these tubes with the experimenter, the female came back to the common mesh wall and gave a cube directly to the male. The female grabbed again four tubes out of sight of her partner. Later, the male took a branch and gave it to the female, followed by a tube. Finally, once the female had exchanged this tube with the experimenter, she gave two cubes directly to the male, who exchanged them with the experimenter. The whole exchange event took place within 14 min.

Considering the previous likely instance of reciprocal exchange, we checked whether reciprocity might occur within each pair of orangutans tested even if gift reciprocity did not arise at the group level. We did not find any statistically significant correlations between the number of tokens given and received for partner-valued tokens or for no-value tokens among the 12 sessions for any pair of individuals.

Because reciprocity did not appear during other testing sessions, we studied the possibility that gifts could be correlated to social interactions between the subjects when they were back in their social group. Affiliation levels between group members did not explain the gifts observed during testing sessions; number of tokens given were not significantly correlated with the number of scans of allogroom, physical contact, and proximity between apes (Dietz's test; p = .685, rs = −.13) as the number of tokens received (Dietz's test; p = .646, rs = −.13).

Discussion

All great ape species learned to exchange the correct tokens with the experimenter. Because transfers in bonobos resulted from a single bonobo's tendency to play, orangutans were the sole species in which transfers occurred consistently. Those transfers, however, were not reciprocal. Only once did we observe an episode involving repeated alternated gifts between a pair of orangutans that might have represented an instance of calculated reciprocity. We found little evidence suggesting that apes took into account the value of the tokens for their partners. Instead, they appeared to transfer tokens spontaneously or in response to gestural requests such as hand begging or pointing toward a particular token. Gifts of tokens were not part of a larger interchange system including social interactions; we found no evidence that the number of gifts was related to the level of affiliation between individuals.

Some abilities required for calculated reciprocity are, however, present in great apes. All four species showed an ability to actively give a token to a conspecific partner. An active gift was the most frequent type of transfer recorded, particularly among orangutans, which sharply contrasts with earlier reports of transfers between conspecifics; in captive capuchin monkeys and chimpanzees, the most commonly reported form of transfer is passive, that is, one individual obtains an item from another without the initial possessor's active help (de Waal, 1989, 1997). In the wild, most transfers between two conspecifics are passive, as in food-sharing and tolerated theft (see Feistner & McGrew, 1989, for review). After chimpanzees' hunting, for example, a possessor of meat tolerates that a previous helper takes some part of the prey (Mitani & Watts, 2001). This tolerance may be interpreted as an interchange system and places the donor as an active partner. As noted by Stevens and Hauser (2005), however, allowing another individual to take appears to be psychologically different from giving. For passive transfers, the calculation between gift and return should not be overestimated, and this result should be considered with caution. Conversely, the occurrence of active gifts in our study indicates that all great apes can intentionally give a good to another when needed.

In earlier studies, active transfers mainly consisted of one individual's laying a good down (Beck, 1973; de Waal, 1997, 1993; Paquette, 1992; Westergaard & Suomi, 1997). Here, we label such transfers *passive*. We observed active transfers, though; they were either indirect gifts when an individual placed a token in the partner's compartment without any physical contact between individuals or direct gifts when one individual delivered a token into the partner's hand or mouth. Indirect gifts were the most frequently observed in three of the four species tested: gorillas, chimpanzees, and bonobos—provided that Yas's unintentional transfers were not taken into account. By contrast, most orangutans' gifts were direct. Such transfers are scarcely observed in nonhuman primates, some have been reported in a few studies involving capuchin monkeys (de Waal, 1997; Westergaard et al., 2007) and symbol language–trained immature chimpanzees (Savage-Rumbaugh et al., 1978). In our study, orangutans appeared to be the only species in which calculation might sustain the gifts observed.

Captive great apes experience physical barriers, so they regularly develop gestures to request desirable but unreachable food and objects from humans (Leavens, Hopkins, & Bard, 2005; see Call & Tomasello, 2007, for a review). Such gestures typically involve the extension of an arm or a hand in a behavior recalling human begging by holding out a hand or pointing gestures. Although most pointing episodes have been observed between nonhuman apes and humans, there are two studies in which pointing occurred between two nonhuman apes. Savage-Rumbaugh (1986) observed a chimpanzee request food from another chimpanzee on repeated occasions during a cooperative task in the laboratory. Veà and Sabater Pi (1998) observed a juvenile bonobo in the wild pointing toward a bush where humans were hiding. In contrast, some form of holding out the hand occurs in food transfers between adults in both captive and wild apes (chimpanzees [Teleki, 1974; van Hooff, 1974], bonobos [de Waal, 1988; Kano, 1992, 1998], and gorillas [Pika, Liebal, & Tomasello, 2003]). Among orangutans, this behavior has mostly been observed among infants begging food from their mother both in the wild and in captivity (Liebal, Pika, & Tomasello, 2006; Rijksen, 1978). In our study, this behavior was not restricted to the mother–infant relationship and occurred between unrelated individuals. Except for gorillas, individuals of each species tested in our study requested tokens by either pointing or holding out the hand, attempting to elicit cooperation from their partner, even though orangutans produced the vast majority of the observed instances. Such occurrences support the view that subjects understood the experimental situation, that is, that they could obtain additional tokens by getting them from their partner. Again, orangutans performed many more begging gestures compared with other apes species, increasing the potential for cooperation from the partner.

The social life of gorillas is characterized by low levels of interactions (Watts, 1996, 2003). Thus, it is understandable that in this study they displayed low rates of gestural communicative signals such as holding out the hand. The lower number of direct gifts and begging gestures recorded in chimpanzees and bonobos than in orangutans is more surprising in view of the mainly solitary life of the latter in the wild, although it has been argued that orangutans are social animals living in an extended social system (Galdikas, 1984; van Schaik & van Hooff, 1996). Nonetheless, bonobos and chimpanzees live in a fusion–fission society (Badrian & Badrian, 1984; Goodall, 1986; White, 1988) in which they face direct competition for mates and food resources (Hare, 2001). They may perceive conspecifics more often as potential competitors than as potential cooperators. The need to out-compete may restrain the emergence of cooperation (Hare, 2001). Recent studies on chimpanzees' cooperation have provided rather contradictory results. Chimpanzees failed to understand the cooperative pointing gesture emitted by a cooperator toward a baited bucket (Herrmann & Tomasello, 2006). Although chimpanzees revealed other-regarding behaviors in nonfood situations (Warneken & Tomasello, 2006) and could solicit partners in a cooperation task (Crawford, 1937), they failed to show altruistic or other-regarding behavior toward conspecifics in food-acquisition situations (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005). Moreover, captive chimpanzees readily solicit help from a human partner, but not from a conspecific (Hirata & Fuwa, 2007).

Compared with other great apes, orangutans face less direct competition on a daily basis (Shumaker, Palkovich, Beck, Guagnano, & Morowitz, 2001). The significant number of gifts recorded in orangutans might underline a greater ability of the individuals to interact with partners, to give, to beg, and to cooperate if not to exchange. Although variations in the social behaviors of the four species tested may partly explain the contrasts found in their rates of gifts, this intriguing result still needs confirmation. It represents a limited number of individuals differing in their developmental history. Further studies with a larger number of individuals and groups will have to confirm that orangutans are more prone to beg and give than other great apes.

The analysis of the gifts performed by orangutans brings insights about their abilities to understand their partner's needs. Economical exchanges are likely to increase when each side knows how partner values the traded item. No doubt the orangutans knew the value of their own tokens because they successfully selected them when exchanging with the experimenter. Knowing whether they understood the value of the token attributed to their conspecific partner is not so clear. We analyzed the gifts after pointing gestures toward tokens and after holding out the hand to the partner. These two behaviors were shown to increase the number of gifts. We found a larger number of valuable tokens were received after pointing, whereas holding-out-hand behavior—that is, directed toward the partner and not toward tokens—was followed by gifts of valuable tokens as often as gifts of nonvaluable ones. From these results, we conclude that donors probably did not understand which tokens were meaningful to their partner.

The occurrence of pointing behavior between orangutans is another intriguing result of our study. Although pointing often occurs in captive apes interacting with humans (Leavens & Hopkins, 1999; Tomasello, 2006), it is generally not reported between two individuals of the same species (but see Savage-Rumbaugh, 1986; Veà & Sabater Pi, 1998). Orangutans had been already trained to point by keepers or human experimenters in previous cognitive tasks, but not in our study. The subjects were not observed pointing at tokens when interacting with the human experimenter, but they did so when interacting with a conspecific. Such instances of pointing appeared to have an imperative motivation ("Give me this"), not a declarative one ("look at this"; Call & Tomasello, 2007; Gómez, Sarrià, & Tamarit, 1993). The recipients of pointing appeared to understand this gesture as a request because they transferred the partner-valued tokens more often than in the absence of pointing. However, these request–comply routines that included the participation of gestures did not develop into full-fledged reciprocal exchanges. Before conventional exchanges, *Hominini* reciprocity may have been partially restrained by social constraints like those found in nonhuman primates. Prosociality and intentional giving likely played an important role in the hominization process (Stoczkowski, 1994), making possible the emergence of complex social rules of exchange based on reciprocity.

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