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Animal behaviour

Calculated reciprocity after all: computation behind token transfers in orang-utans

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Transfers and services are frequent in the animal kingdom. However, there is no clear evidence in animals that such transactions are based on weighing costs and benefits when giving or returning favours and keeping track of them over time (i.e. calculated reciprocity). We tested two orang-utans (*Pongo pygmaeus abelii*) in a token-exchange paradigm, in which each individual could exchange a token for food with the experimenter but only after first obtaining the token from the other orang-utan. Each orang-utan possessed tokens valuable to their partner but useless to themselves. Both orang-utans actively transferred numerous tokens (mostly partner-valuable) to their partner. One of the orang-utans routinely used gestures to request tokens while the other complied with such requests. Although initially the transfers were biased in one direction, they became more balanced towards the end of the study. Indeed, data on the last three series produced evidence of reciprocity both between and within trials. We 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.

Keywords: reciprocal giving; exchange; bartering; economics; primates

1. INTRODUCTION

Economics in human societies constitute a notable anomaly compared with the animal kingdom. While there are numerous examples of reciprocal transfers of services among animals (Dugatkin 1997), there is little experimental evidence that such transfers rely on calculated reciprocity, i.e. weighing costs and benefits when giving or returning favours and keeping track of those transactions (de Waal & Luttrell 1988). This absence is particularly puzzling because monkeys and apes possess cognitive prerequisites for calculated reciprocity including memory for past interactions, tolerance to delay of gratification and they can readily exchange tokens or food with humans (e.g. de Waal 1989; Westergaard *et al.* 2007).

Although passive food transfers are frequently observed among conspecifics (Mitani & Watts 2001), active transfers are much less frequent (de Waal 1997) and reciprocal food transfers are virtually non-existent in non-human primates. As stressed by Hemelrijk (1996), the correlations observed in the reciprocity of positive behaviours are not sufficient to conclude on the calculation that would sustain this reciprocity. Instead, most transfers may rely on symmetry-based or attitudinal reciprocity (Brosnan & de Waal 2002), two forms of reciprocity where no calculation is involved. Studying active transfers is the best way to assess whether individuals calculate their own losses and gains and keep track of them over time. Capuchin monkeys (*Cebus apella*) were recently shown to exhibit active transfers of tools but the recipient never returned a share of the reward to the donor (Westergaard *et al.* 2007). Savage-Rumbaugh *et al.* (1978) reported cases of direct transfers of tools in young chimpanzees (*Pan troglodytes*), which could be based on computation. Transfers involved subsequent sharing of food and role alternations in both individuals. Subjects in this study were young chimpanzees, symbol-language trained and more likely prone to cooperate than adult wild chimpanzees.

To qualify reciprocal giving as 'calculated giving with return expectancy', it must be shown that (i) giving occurs intentionally from one partner to another, (ii) partners know the value of the traded items for both sides and (iii) partners expect given items to be returned. Directly transferring to the partner's hand or mouth the items, which the donor selected among the available alternatives and which are useful to the partner but useless to the donor, indicates that the donor's actions are intentional and based on knowledge about the value of items for her partner. Return expectancy can only be assessed by the capacity of the donor to adapt to the partner's behaviour. For example, generous donors should give less and less if their transfers are never or infrequently returned, conversely less cooperative individuals should give more and more to secure or maintain their partner's cooperation. Ultimately, a balance should be reached between partners' giving and receiving.

Recently, we have compared the propensity of gorillas (*Gorilla gorilla*), orang-utans (*Pongo pygmaeus abelii*), bonobos (*Pan paniscus*) and chimpanzees to spontaneously exchange tokens of different values with a conspecific (Pelé *et al.* in press). Self-value tokens received from a partner could further be exchanged for food with the experimenter. Orang-utans exhibited the highest number of token transfers. One pair of orang-utans exhibited reciprocal transfers although those transfers were mostly biased in one direction. The present study aimed at exploring whether the propensity to give in orang-utans may depreciate over time and trial repetition owing to a lack of reciprocity or, instead, evolve towards balanced exchanges.

2. MATERIAL AND METHODS

Two orang-utans (*Pongo pygmaeus abelii*), a male (Bim, 26 years old) and a female (Dok, 15 years old) socially housed at the Wolfgang Köhler Primate Research Center, Leipzig Zoo (Germany) were tested. Prior to the present experiments, they had been tested

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Table 1. Number and direction of active and passive transfers per individual (excluding the offspring) as a function of the token value. (Asterisks indicate that the observed distribution deviated from 50 : 50 (binomial test: $^{*}p<0.01$; $^{**}p<0.001$). Shown in parentheses are the transferred non-token items (valuable: banana peels; valueless: papers, straws and sticks).)

	Dokana → Bimbo			Bimbo → Dokana		
	type of token			type of token		
type of transfer	valuable	valueless	total	valuable	valueless	total
active	59^{**}	25 (2)	86	19 $(14)^{*}$	6 (8)	47
passive	79^{**}	1	80	2	0	2
total	138^{**}	28	116	35^{*}	14	49

in various cognitive tasks. Dok's offspring, a juvenile male named Pag (also the son of Bimbo), remained with her during testing. Despite being close affiliates, the male and the female were not normally seen sharing food or sitting together.

In a previous study, both subjects had been trained individually to exchange one of three types of tokens for food. A first series of trials conducted one month after the end of the previous study served as a refresher of the exchange procedure and consisted of 12 trials. In this series, both subjects entered their own side of a room divided by a mesh through which they could transfer tokens to each other. Prior to subjects entrance, a set of 36 tokens had been left in each compartment: 12 *self-value tokens*, exchangeable with the experimenter for food, 12 *partner-value tokens* that only their partner could exchange for food and 12 *no-value tokens* for which both subjects received nothing. In the following three 12-trial series, each subject received only 12 partner- and 12 no-value tokens. Thus, each subject first needed to obtain their self-value token from their partner. Subjects were tested at the rate of one trial per day. In the first 3 min, partner could exchange their self-value token with the human experimenter (series 1) or start exchanging tokens with the partner (series 2–4). Then the experimenter left the room for 3 min to avoid influencing possible transfers between subjects and returned afterwards for a minimum duration of 3 min. Whenever transfers of valuable tokens occurred between subjects, the experimenter requested and exchanged them for food. A trial ended when transfers did not occur after 6 min. We recorded active transfers (placing a token into the hand, mouth or cage of the partner) and passive transfers (placing the token in her own cage but near the mesh so that the partner could take it). We also observed transfers of edible (banana peel) and non-edible items (paper, straw). Since edible items were eaten upon receipt and non-edible items were discarded, we treated them as tokens and included them in the analyses.

3. RESULTS

We observed 215 transfers between the two individuals in the course of the four series (48 trials). Table 1 presents the number of active and passive transfers per individual as a function of the token value. The male mostly used active transfers, whereas the female displayed a similar number of active and passive transfers. However, most of the female passive transfers concerned partner-valuable tokens, which she displaced towards the cage fence within the male's reach. In particular, she displaced 63 and 19 partner-valuable and partner-valueless tokens near the fence, respectively. Both subjects transferred more partner-valuable tokens to their partner than non-valuable ones (binomial test, $p<0.001$; see the electronic supplementary material). This result remained unchanged after restricting the analysis to the active transfers (binomial test, $p<0.001$).

Figure 1 presents the number of valuable tokens transferred according to series. Although initially transfers were biased in favour of the male (binomial test: $p<0.001$), values converged over time until no significant difference was found in the last series (binomial test, $p=0.1$). Interestingly, the overall number of valuable transfers remained largely unchanged across series ($n=48$, 42, 39 and 44, respectively).

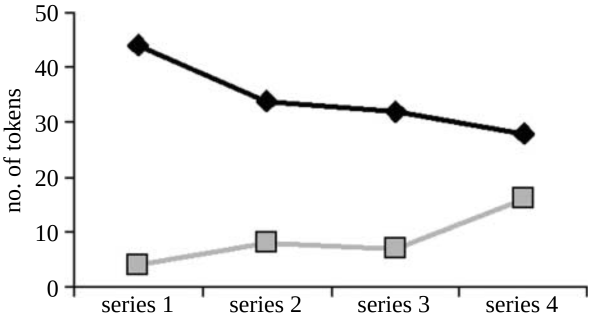

Figure 1. Number of partner-value tokens (including banana peel) transferred by individuals (excluding the offspring) in each of the four series (diamonds, Dok; squares, Bim).

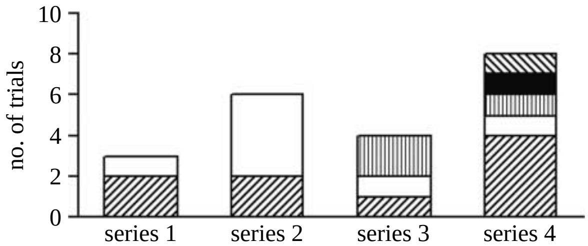

Figure 2. Occurrence of reciprocity and length of consecutive turn-taking per trials between donor and recipient in each of the four test series (excluding the offspring; left-hatched bar, five turn taking; black bar, four turn taking; vertical striped bars, three turn taking; white bars, two turn taking; right-hatched bars, one turn taking).

When considering only the last three series where individuals had to obtain their self-value token from their partner, we found a significant correlation between the number of partner-value tokens received and given (Kendall rank correlation test, $\tau=0.244$, $Z=2.09$, $p=0.036$, $n=36$). From series 2, we also observed an increase in the number of bilateral transfers of valuable tokens involving at least one turn taking compared with series 1 (three transfers in series 1, and 6, 4 and 8 transfers in the following three series, respectively; figure 2). Moreover, the successive turn takings occurring within a trial increased from a maximum of two in series 2 to a maximum of five in series 4. Reciprocation of valuable tokens was not immediate; there was some time delay between receiving and giving back a valuable token (the male: 15–236 s, mean = 84 s; the female: 21–544 s, mean = 149 s). This delay includes the time needed to exchange the token with the experimenter and eat the reward.

The use of gestural communication (pointing and holding-out-hand) differed between the two subjects. The male routinely pointed to tokens (241 times) and held his hand out in the direction of tokens (21 times) to request transfers. His total number of begging gestures increased over time (series 1, 35; series 2, 55; series 3, 82; series 4, 90) yet the percentage of times that begging led to the return of a valuable token sharply decreased over successive series (52.3, 14.3, 16.1 and 12.1%, see the electronic supplementary material). By contrast, the female rarely gestured (one pointing; four holding-out-hands) to request tokens. In addition to the transfers reported earlier, we observed supplementary transfers between the male and the female's offspring. Overall, the female's son transferred a total of 23 tokens (21 of them valuable) to the male whereas the male transferred 8 tokens to the offspring (6 of them valuable). The female took all the valuable tokens from her son upon receipt. The offspring began transferring and receiving tokens from the male in series 2 and 3, respectively. One sequence of transfers between the male and the offspring reached a maximum of four consecutive turn taking within a trial in series 4.

4. DISCUSSION

Both adult orang-utans actively transferred numerous valuable tokens to their partner. This result contrasts with the reports that another ape species, chimpanzees, mainly fail to show prosocial behaviours in an experimental set-up (Melis *et al.* 2008; Vonk *et al.* 2008). However, orang-utans may differ from more prosocial species such as capuchins where giving seems to be self-rewarding (de Waal *et al.* 2008), since they transfer tokens based on computation and return expectancy. Although the transfers were initially biased in one direction, they became more balanced towards the end of the study; data from the last three series produced evidence of reciprocity both between and within trials. We observed an increase in the occurrence and length of consecutive turn taking. This is the first experimental demonstration in non-human primates of the occurrence of calculated reciprocity through the repeated exchanges of goods. It is currently unclear whether simply increasing the number of trials or slightly changing the procedure by compelling orang-utans to exchange with their partner to get valuable tokens was the reason for the appearance of a more sophisticated token transfer system. The intentionality behind giving, the computation based on expected returns, in addition to the shared knowledge of the value of the traded items showed that calculated reciprocity underpinned the transfers of goods.

Orang-utans are known to modify their gestural signals according to the comprehension of their human audience (Cartmill & Byrne 2008). Gesturing to communicate one's needs and complying with requests of their partner show that subjects understood the need of each other and may have used gestural signals to elicit faster responses. Gesturing may have been instrumental in, at least jump starting, the reciprocal transfers. Indeed, communication became less effective over time either because each partner's needs were mutually understood or the female stopped honouring all requests perhaps to press the male into transferring her tokens. An unexpected result was that the juvenile orang-utan spontaneously started transferring and receiving tokens (mostly valuable) from the adult male. The involvement of the juvenile individual may have additionally created some partner-choice opportunities, transforming an initially bilateral situation into a market-like one (Noë 2005). It may have modified the balance of supply and demand. The female often stole the tokens received by her offspring from the male preventing further comparison with a multi-partner trading situation.

Human societies have built complex social networks based on language and cultural norms. Economic trade is another route for complex exchanges between individuals that rests on the mutual comprehension of the value of traded goods and tracking the flow of transactions. Calculated reciprocity may play a similar role in species not relying on language or culture, and provide a further way to extend relationships beyond the affiliative network. Future studies should confirm and extend our results to further individuals and species in more natural contexts. Special attention has to be paid to social tolerance, communication, and request compliance and to the abilities to understand others' needs, which are liable to foster the appearance of mutual exchange.

The work with animals was done according to the principles and guidelines of the German regulations for the treatment of experimental animals.

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