Food transfers in capuchin monkeys: an experiment on partner choice

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Although most primates live in groups, experiments on reciprocity usually test individuals in dyads. This could hide the processes emerging in richer social settings, reducing the ecological validity of the results. We run an experiment on reciprocal food transfers testing capuchin monkeys (Cebus apella) in triads, so that subjects could choose to allow access to their food to either of their two partners. We tested the hypothesis that partner choice was related to a comparison of long-term social bonds with the two partners, more than to a comparison of recent food transfer events from the two partners. The results confirmed this hypothesis, thus supporting the notion that reciprocal partner preferences are based on long-term accounts of benefits that have been exchanged.

Keywords: cooperation; reciprocity; partner choice; social bonds; capuchin monkeys

1. INTRODUCTION

Reciprocity is possibly the most debated among the mechanisms explaining the evolution of cooperation [1]. While scientists agree that reciprocity constitutes a theoretically plausible explanation for the evolution of cooperative behaviours, its actual prevalence among nonhuman animals is controversial [2,3], with sceptics highlighting the rarity of convincing examples and the presumed cognitive complexity necessary to sustain reciprocation [2,4]. Disagreement among scientists stems also from a failure to recognize that two different decision-making processes can be involved in reciprocity [5,6]. First, an animal can behave cooperatively towards a partner in relation to how the partner has behaved towards it before, regardless of the behaviour of other potential partners [7] (we label this ‘within-dyad temporal relations between events’; [6]). Second, an animal can behave cooperatively towards one partner rather than another (‘partner choice’; [8]) on the basis of a comparison of how these partners have behaved towards it before. Available evidence suggests that the latter process is more common and has stronger effects than the former [6].

Typically, these two processes are explored on different time-scales. While the former is tested by examining the relations between events over short time-scales (minutes to hours; [9]), the latter is tested by examining partner choice over much longer time-scales (months; [6]). The choice of these different time scales is based on the assumption that the two decision-making processes differ in their tempo.

Testing within-dyad temporal relations between events over short time-scales assumes that an animal decides to behave cooperatively towards a given partner in relation to how this part has behaved in the recent past more than in the distant past. Available evidence, however, suggests a more complex picture. Although recent events do affect the likelihood to behave cooperatively [9], animals also accept short-term imbalances in their within-dyad exchanges. Overall, long-term exchanges are often more balanced than short-term exchanges [10,11].

Testing partner choice, based on benefits received over long time-scales, assumes that animals decide to behave cooperatively towards a given partner rather than another (partner choice) by comparing long-term ‘accounts’ (do not obviously imply actual calculations; [3]) of benefits received by the two partners more than by comparing recent events. This assumption hinges on the hypothesis that the proximate mechanism underlying partner choice is what Schino & Aureli [3] termed emotional bookkeeping. They suggested that the exchange of cooperative behaviours triggers partner-specific emotional variation, and that partner choice is then based on the emotional states associated with each potential partner. The development of differential social bonds with individual group members would thus constitute an emotionally-based bookkeeping system in which emotions provide the basis for social choices. Under the emotional bookkeeping hypothesis, partner choice must necessarily be based on long-term accounts of cooperative behaviours exchanged because the development and subsequent update of social bonds probably require extensive interactions.

Although we know that long-term reciprocal partner preferences exist [3], the time frame taken into account by the decision-making process of partner choice has never, to our knowledge, been investigated (see [12] for a related issue). The aim of this study was to test the hypothesis that partner choice in cooperative exchanges is affected by a comparison of long-term social bonds with the available partners more than by a comparison of recent cooperative events. To achieve this aim, we adapted the food-sharing experimental set-up of de Waal [13] and gave our subjects the choice among two different partners with whom to interact. We also replicated the experiment of de Waal [13] involving a single partner in order to confirm that our experimental set-up did allow the expression of short-term reciprocation.

2. MATERIAL AND METHODS

(a) Subjects and housing

We tested the members of a group of tufted capuchin monkeys (Cebus apella) numbering 11 individuals (four males and seven females, aged 5–22 years), living at the Istituto di Scienze e Tecnologie della Cognizione, Rome, Italy. With the exception of the alpha male (that was unrelated to all other group members), all other subjects belonged to two matrilines.


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We conducted: (i) a dyadic experiment (involving two monkeys), and (ii) a triadic experiment (involving three monkeys). For both experiments, each session consisted of two consecutive phases, each lasting 7 min. Food (apple pieces) was placed in the bowl(s) outside compartments as described later in text. Food provided was abundant and was rarely consumed entirely. This implied that food transfers had little cost for the ‘owner’ and some benefit for the partner(s).

Experimental sessions were videotaped and behavioural data were later scored from the tapes. We recorded successful food transfers from one individual to the other and tested the relations between the amounts of food transferred in the two experimental phases. Behavioural definitions are given in the electronic supplementary material, table S1.

(c) Dyadic experiment
Each experimental session involved one subject and one partner. At the beginning of phase 1, the partner was given food in the bowl attached to its compartment, whereas the subject was not. In phase 2, the subject received food, whereas the partner did not. Twenty different dyads were tested. Each dyad was tested six times, over six different days.

(d) Triadic experiment
Each experimental session involved one subject and two partners. The subject was in the central compartment, and the two partners in the two lateral compartments. The two partners were matched as far as possible in terms of sex, dominance rank and kinship with the subject, so as to minimize differences in relationship quality (see later text and the electronic supplementary material for details). At the beginning of phase 1, the two partners were given food in their bowls, whereas the subject was not. In phase 2, the subject received food and the partners did not. Ten different triads were tested. Each triad was tested six times, over six different days.

(e) Group observations
Behavioural observations were conducted for total of 50 h while the group was in its outdoor enclosure. Focusing on the entire group, the observer recorded all occurrences of grooming and aggression, along with the identities of the individuals involved (see the electronic supplementary material for details).

(f) Data analysis
Analyses tested the relations between food transfers to and from subjects and partners in the two phases of the experiments, along with the effect of relationship quality. For each subject–partner dyad, a relationship quality score was obtained by subtracting the rate (episodes per hour) of aggression exchanged from the rate of grooming exchanged during group observations. Thus, a high relationship quality score characterized dyads that exchanged frequent grooming and rare aggression, whereas a low relationship quality score characterized dyads showing the reverse pattern. Subject–partner food transfers were measured either as absolute values (in both experiments) or as differences from the other partner (only in the triadic experiment). Relationship quality scores were measured as differences from the other partner and entered only in the analysis of the triadic experiment. Differences between the two partners, being a comparative measure, provide an index of the subject's partner choice. Statistical analyses were based on either within-dyad or across-dyad regressions (see the electronic supplementary material for details). Note that within-dyad variations in food transfers (i.e. variations across trials of the same dyad) cannot be explained by variations in relationship quality, because each dyad had, obviously, only a single relationship quality score.

3. RESULTS
(a) Dyadic experiment
Within dyads, variation in the food transferred from the subject to the partner during phase 2 of the experiment was positively related to the food the subject got during phase 1 (coefficient = 0.296,  t_{44} = 2.76,  p = 0.008; effect size  r = 0.384).

(b) Triadic experiment
Similar to the dyadic experiment, in the triadic experiment, within-dyad variations in the food transferred from the subject to each of the two partners during phase 2 of the experiment were positively related to the food the subject got during phase 1 (coefficient = 0.148,  t_{103} = 2.01,  p = 0.048; effect size  r = 0.194), although the effect was weaker.

Then, we tested partner choice (i.e. expressed the data as the difference from the other partner) in an across-dyad analysis that also allowed the assessment of the role of relationship quality. Differences in the food transferred during phase 2 were not significantly related to differences in the food transferred in the opposite direction during phase 1 (coefficient = 0.078,  z = 1.06,  n = 120,  p = 0.291). By contrast, differences in the food transferred were significantly related to differences in the quality of the social relationship the subject had with the two partners (coefficient = 0.266,  z = 3.16,  n = 120,  p = 0.002; figure 1).

4. DISCUSSION
In this study, we modified the experimental paradigm of de Waal [13] and allowed our subjects to interact with multiple partners. This set-up more closely resembles natural conditions, where the animals can...
choose which partner(s) to interact with among numerous group companions. Also, in contrast to the extreme artificiality of most of the experimental settings used to investigate reciprocity, this set-up allows some degree of experimental control while maintaining the ecological validity and (presumably) emotional salience of cooperation in naturalistic settings [3].

Our study had three main findings. First, in dyadic tests, food transfers received predicted food transfers given, showing that short-term temporal relations between food transfer events provided an explanation for the exchange of these cooperative behaviours. Second, within-dyad temporal relations between food transfer events weakened considerably in triadic tests. Third, partner choice was based on the comparison of long-term social bonds, whereas the comparison of recent food transfer events played little or no role.

Our first finding confirms previous observations [13] and adds to the literature on reciprocal altruism by showing that even subtle cooperative behaviours such as tolerated taking of food can be reciprocated. Tolerance has been repeatedly suggested as constituting a crucial component of primate social relationships, but it remains little investigated [14]. Interestingly, our second finding shows that short-term temporal relations between cooperative events were considerably weakened when the presence of a third individual allowed partner choice (as shown by the effect sizes in the within-dyad analyses of the dyadic and triadic experiment). This may contribute to explain the difficulty in demonstrating reciprocal altruism in naturalistic settings.

Our third finding is particularly relevant as it provides experimental support for the assumption that animals make their partner choices on the basis of comparisons of long-term social bonds more than of comparisons of short-term exchanges. Notably, the stronger effect of social bonds was apparent despite our effort to minimize between-partner differences in terms of relationship quality with the subject. Our results are also consistent with those reported in chimpanzees, which did not cooperate preferentially with the partner that had recently helped them [15]. The authors hypothesized that long-term social preferences could not be overcome by recent experience during the experimental task, but could not test this hypothesis.

Indirectly, our findings also provide support for the hypothesis that emotional bookkeeping provides the proximate mechanism underlying partner choice [3]. Long-term accounts of cooperative exchanges based on detailed memories of multiple events, and calculations of cost/benefit ratios are cognitively demanding and are consequently difficult for non-human animals. Emotional bookkeeping, by contrast, provides a cognitively inexpensive solution to the need to recognize and choose valuable partners that we predict will be found to be taxonomically widespread.

All procedures complied with protocols approved by the Italian Health Ministry (Licence no. 63/2007-C) and were performed in full accordance with the European law on humane care and use of Laboratory animals.

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