RESEARCH ARTICLE

Inequity Aversion in Relation to Effort and Relationship Quality in Long-Tailed Macaques (*Macaca fascicularis*)

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Social animals may employ evolved implicit rules to maintain a balance between cooperation and competition. Inequity aversion (IA), the aversive reaction to an unequal distribution of resources, is considered such a rule to avoid exploitation between cooperating individuals. Recent studies have revealed the presence of IA in several nonhuman species. In addition, it has been shown that an effort is crucial for this behavior to occur in animals. Moreover, IA may well depend on the partner's identity. Although dominant individuals typically monopolize food, subordinate individuals obtain less preferred food and usually do not protest. Furthermore, "friends" may pay less attention to equity than "nonfriends." We tested whether long-tailed macaques show IA with different cost–benefit ratios. In addition, we determined whether IA depends on relationship quality (RQ). Dominant subjects expressed IA only when a small effort was required. At a very large effort, however, long-tailed macaques did not show IA, possibly owing to bottom effects on the number of rewards they aim to receive. Moreover, and contrary to our predictions, an individual's inequity response was similar when tested with a "friend" or a "nonfriend." Therefore, we conclude that long-tailed macaques show IA only in conditions of moderate effort, yet that IA seems independent of RQ. Furthermore, IA may not be domain specific. Altogether, IA may be a trait present in all species that habitually cooperate, independent of their social organization. Am. J. Primatol. 74:145–156, 2012. © 2011 Wiley Periodicals, Inc.

INTRODUCTION

Cooperation exists in a myriad of varieties, although it can only be evolutionarily stable when the reward received by participants at least equals the effort put in. The pay-off of cooperative acts is thus important for the individuals involved. Cooperating individuals may avoid exploitation by using cognitively complex decision rules to monitor own and their cooperator's pay-off. Humans are considered highly cooperative [Fehr & Fishbacher, 2003] and they prefer an equal pay-off of effort and reward in a cooperative act, and react aversive to unequal pay-offs, a preference known as inequity aversion (IA) [Adams, 1963]. Humans may react aversively when they obtain fewer benefits than the other individual, i.e. disadvantageous IA or less prevalent, when they obtain more benefits than the other individual, i.e. advantageous IA [Fehr & Schmidt, 1999]. To avoid confusion and to be consistent with the animal literature on this subject, we will use in the remainder of the text Inequity Aversion (IA) when we refer to disadvantageous IA. When we refer to the rare advantageous IA we will use the full term.

Until recently, IA was considered uniquely human. Yet, besides humans, animals of numerous species cooperate with conspecifics. Especially, species living in complex social systems with recognized individuals may have evolved a similar strategy to keep track of the balance in rewards received and given within a cooperative act. Accordingly, in their seminal article, Brosnan and de Waal [2003] found that brown capuchin monkeys (*Cebus apella*) also show IA. These monkeys refused to perform a task or rejected the reward when the monkey sitting next to them received a qualitatively better reward for the same task.

Others, however, could not replicate the original findings in capuchin monkeys [Dubreuil et al., 2006; Roma et al., 2006], and consequently IA in animals became a highly debated subject [Bräuer et al., 2009; Dubreuil et al., 2006; Roma et al., 2006; Wynne, 2004]. The results of Brosnan and de Waal [2003] claimed to depend on frustration effects [Bräuer et al., 2006; Dubreuil et al., 2006; Roma et al., 2006]. Yet, when controlling for such effects, a similar reaction to inequity was still found in these capuchin monkeys [Brosnan & de Waal, 2006]. More importantly, it was shown that performing a task in order to obtain the reward is considered crucial for IA [Brosnan & de Waal, 2006; Brosnan et al., 2010; van Wolkenten et al., 2007], a precondition that was lacking in those studies that failed to replicate the original findings [Dubreuil et al., 2006; Roma et al., 2006].

IA has now been reported for chimpanzees (*Pan troglodytes*) [Brosnan et al., 2005; see also Bräuer et al., 2009], cotton-top tamarins (*Saguinus oedipus*) [Neiworth et al., 2009], and domestic dogs (*Canis familiaris*) [Range et al., 2009a]. Moreover, when given the choice, brown capuchin monkeys [Fletcher, 2008], chimpanzees [Melis et al., 2009], and cotton-top tamarins [Cronin & Snowdon, 2008] prefer an equitable distribution of rewards. Altogether, these studies indicate that IA in animals is not an artifact, but a rule found in at least some animal species.

All the species that show IA are known for their cooperative skills. Interestingly, IA is not present in orangutans (*Pongo pymaeus*) [Brosnan et al., 2011] and squirrel monkeys (*Sairmiri* spp.) [Talbot et al., 2011], species that do not habitually cooperate. Therefore, taken together, these results may indicate a coevolution of IA and cooperation [Brosnan, 2011].

Cooperation, however, is not a unitary phenomenon and the tendency to cooperate will vary between group members. Therefore, individuals may differ in how they employ mechanisms proposed to regulate cooperation, such as IA. First, it may depend on the context in which animals show cooperation. Cooperation can serve many functions, from cooperative hunting [e.g. Boesch & Boesch-Achermann, 2000] to coalitions to dethrone a dominant individual [Noë & Sluijter, 1990]. Second, the tendency to cooperate depends on one's own position in the group [van Schaik et al., 2004]. Third, the tendency to cooperate depends on the relationship with the partner [Melis et al., 2006]. Therefore, conditions in which IA will be found may depend on the nature of the paradigm, position of the partners in the dominance hierarchy, and partner identity.

In accordance with previous results concerning IA in animals [Brosnan & de Waal, 2006; Brosnan et al., 2010; Neiworth et al., 2009; van Wolkenten et al., 2007], we first hypothesize that IA will be more pronounced when work is involved than when animals are just unequally provisioned. Furthermore, we expect that IA will increase with increasing workload. In addition, inequity can be defined in both reward and effort when work is involved [Adams, 1963]. Therefore, we hypothesize that IA will be most pronounced when work is involved, and in addition to an unequal reward distribution, also the amount of effort needed to receive a reward is unequally distributed.

Second, we hypothesize that if IA is domain specific, only those species that cooperate to obtain food (i.e. cooperative hunting), e.g. capuchin monkeys [Rose, 1997], chimpanzees [Boesch & Boesch-Achermann, 2000], wolves (*Canis lupus*) [Mech, 1970], or at least share food, e.g. capuchin monkeys [Perry & Rose, 1994], chimpanzees [Boesch & Boesch-Achermann, 2000], and tamarins [Feistner & Price, 1999] will pass the IA tests in the food domain. IA aversion has only been tested with a food paradigm. If, however, IA is not domain specific, not only species that cooperate in the food domain, but also species that cooperate in the social domain (e.g. show coalitionary support) may express IA in a food paradigm [Brosnan, 2011; cf. Talbot et al., 2011].

Third, we hypothesize that cooperation, and thus IA, may depend on an individual's social position in the group [Chalmeau et al., 1997; van Schaik et al., 2004; Werdenich & Huber, 2002]. In groups with a clear and thus despotic dominance hierarchy, animals often suffer an unequal distribution of food in their everyday lives, where high-ranking individuals have access to the preferred food first, leaving the subordinates with the less preferred food [Sterck et al., 1997; van Schaik, 1989]. In accordance with that, several studies showed that in chimpanzees dominance rank does influence responses to inequity [Bräuer et al., 2006, 2009; Brosnan et al., 2010] and that dominant individuals respond more strongly to inequity than subordinate individuals [Brosnan et al., 2010]. In spite of that, it has also been suggested that despotic species will not show IA [Neiworth et al., 2009]. We, however, expect that dominants of a despotic species will show IA in the presence of a subordinate. Last, we hypothesize that IA like cooperation [Melis et al., 2006] may also depend on the quality of the partners' relationship. In humans, rules for cooperation among friends differ from those with strangers or acquaintances. The relationship between friends is characterized by concern for each other's welfare, benefiting the other when a need exists, and friends will distribute resources mainly according to differences in need, whereas strangers and acquaintances prefer equal distributions [Clark & Mills, 1979; Deutsch, 1975]. Similarly, group-living animals can have differential bonds with group members [Aureli, 1997] and the closest social bonds have been compared with human friendship [Massen et al., 2010a; Silk, 2002; Smuts, 1985]. Also, in animals, it may be in one's own interest to help a "friend," even without a

contingent return [Roberts, 2005]. There are some indications that quality of the participants' relationship is important in the inequity response of chimpanzees [Brosnan et al., 2005] and dogs [Range et al., 2009b]. However, whether it is indeed the relationship quality (RQ) that affects the contingency of exchange processes is still unclear and remains to be tested.

Long-tailed macaques, a highly hierarchical species [Thierry, 2000], are not known to cooperatively share food. However, they do exhibit several cooperative patterns in behavior for which IA may be beneficial. Long-tailed macaques form alliances in aggressive contexts [de Waal, 1977; van Noordwijk & van Schaik, 1985], trade beneficial behaviors reciprocally [Gumert & Moon-Ho, 2008], interchange behaviors on a market place [Gumert, 2007a,b], and can behave prosocially [Massen et al., 2010b, 2011]. Therefore, we expect long-tailed macaques to show IA when underbenefited. This study is designed to test whether long-tailed macaques show IA, whether this depends on effort, and whether the response to inequity depends on the RQ of the dyad tested. The study consists of two experiments. In the first experiment, we established whether long-tailed macaques express IA in three tasks with different effort levels. In the second experiment, we tested the effect of RQ on IA by pairing the subject with both a ''friend'' and a ''nonfriend.''

EXPERIMENT 1: IA IN LONG-TAILED MACAQUES

In our first experiment, we determined whether long-tailed macaques show IA and whether this depends on the effort required to obtain the food reward. Long-tailed macaques show strong contest competition at food patches and form steep linear dominance hierarchies [Sterck & Steenbeek, 1997; van Noordwijk & van Schaik, 1987]. To qualitatively enhance the chance of finding IA, we tested dominant individuals paired with a subordinate partner. In addition, subordinate partners may refuse a qualitative better reward when the dominant subject receives a less preferred reward, because in a natural setting subordinates never dare to take preferred food in the presence of a dominant. Thereby, these subordinates may show advantageous IA. Advantageous IA has been found in chimpanzees, i.e. subjects more often refuse a better reward when their partner receives a less good one than when their partner receives the same better one, and is suggested to be owing to a concern about retribution [Brosnan et al., 2010]. Furthermore, because we expect to find no IA among ''friends,'' we first only tested individuals paired with a partner with whom they did not have a particularly good relationship.

The dominant individuals of these ''nonfriend'' nonkin dyads were tested in three tasks, encompassing seven conditions. The effort level was varied in each task: subject and its partner both did not have to work (i.e. were provisioned), or were both required to work a little, or had to work hard for their reward. The reward of the subject was always the same, yet, either of similar (equity) or of lower (inequity) quality than the reward of its partner. Furthermore, because Adams [1963] defined inequity both in reward and effort, we tested also effort inequity. In this last condition, the subject had to work hard for the less preferred reward, whereas its partner was provisioned with the more preferred reward. These seven conditions allowed us to determine the presence of IA for both effort and reward inequity in this species and the effect of the different effort levels on IA. Moreover, it allowed us to determine whether subordinate individuals show advantageous IA when treated better than their dominant partners.

METHODS
Ethics Statement

The experiments were approved by the Ethical Committee of Utrecht University (DEC 2007.I.08.103), and thus comply with the Dutch law and with the American Society of Primatologists principles for the ethical treatment of nonhuman primates.

Subjects and Housing

All tests were conducted between June 2008 and June 2009. The study subjects were 12 long-tailed macaques that all lived in the same social group at the ''Ethologie station'' of the Utrecht University, The Netherlands. The social group consisted of 33 individuals with males and females from all life stages. The group had split from a larger group in 1994 and has been stable since then; most animals were born in this group. The group was housed in an indoor enclosure ($235 \, m^3$) with access to an outdoor compound ($800 \, m^3$), with plenty of climbing facilities and regular provisioning of enrichment. Water and commercial monkey chow were available ad libitum. Alternately, fruits, vegetables, or bread were daily provided to the group half an hour after the day's testing was completed. This feeding schedule was followed regardless whether the animals participated in a test that day. The animals were never food or water deprived.

The dominance hierarchy in the group and the friendship status among group members were analyzed before the experiments. The dominance hierarchy was determined by analyzing unidirectional submissive behaviors (''bare teeth'' and ''make room'' without prior aggressive behavior) that were observed ad libitum. Results were arranged in a sociomatrix. The dominance order most consistent with a linear hierarchy was determined with MatMan 1.1.4. and the dominance

hierarchy was significantly linear (linearity index: $h' = 0.59$, $P < 0.05$) [de Vries, 1995, 1998]. Rank numbers were assigned with 1 for the most dominant individual and 33 for the least dominant individual. Rank difference was calculated by subtracting the rank number of the subject from that of its partner.

To measure RQ, we conducted time sample scan observations (2–4 times a day, with at least 1 hr between each observation) of all [independent] group members during the 10 months before testing, to assess who was sitting with whom (contact sitting) and who was grooming whom. For each individual, potential friends were individuals in the upper quartile of contact sitting and grooming. Only individuals that score in the highest quartile in both contact sitting and grooming were considered friends. With these rules for friends, we found 25 friends out of a total 497 nonkin dyads. For logistic reasons (i.e. the possibility to create enough novel nonkin dyads), we considered all other dyads as nonfriends.

To test the effect of RQ on the inequity response, we used the data of contact sitting and grooming. We ordered RQ based on the degree of contact sitting and grooming per individual. The individual with whom they sat most often in contact was given number 1 and with whom it sat least often together was given number 33. When an individual sat the same proportion of time together with two individuals, they were given the average number, e.g. if they were 4 and 5, they were both numbered 4.5. The same was done for grooming. For each partner, both numbers were added and divided by two, leading to RQ ordering ranging between 1 and 33.

Subjects and their test partners were adult or subadult monkeys (ranging in age between 3 and 21 years, see supplemental materials) that reliably could pull in a tray of the test apparatus (Fig. 1). Pairs of subject and partner were chosen according to their "friendship status" and difference in dominance rank. A pair of subject and test partner

was never kin or friends, and were furthermore chosen to have a rank difference as large as possible, in which the subject was always the dominant animal.

Based on these conditions, we selected for the first experiment five male–male pairs, five female–female pairs, two male–female pairs, and two female–male pairs. The mean rank difference in the pairs was 12.4 ($\sigma = 7.61$) (for a table of the dyads, see supplemental materials). Although we tried to avoid using animals more than once in the experiment, two animals were used twice as subject, five animals twice as partner, and two animals as both partner and subject. In the analysis, multiple test results of one subject animal were averaged.

Test Environment

The training and testing procedure of the animals was as follows: the complete group entered from their home cage that was connected to the test cage of 32 m^3 (4 m $\times$ 4 m $\times$ 2 m). From this test cage, the subject and its partner entered the test chamber (110 cm $\times$ 55 cm $\times$ 80 cm). The test chamber was divided in half by a transparent lexan screen, to allow visual contact between the two monkeys while keeping them physically separated. During the tests, dependent offspring were allowed into the test chamber with their mothers. Both subjects and partners were trained to be separated in the test chamber and to pull a tray of the apparatus (Fig. 1). Neither subject nor test partner was tested more than once on the same day and there was always at least a day between two conditions for both subject and test partner.

One month before testing, both subjects and their partners participated in a series of food preference tests to determine their preference for a slice of apple over a slice of cucumber and a slice of mango over a slice of cucumber. For each comparison, each animal participated in three series of ten trials, in which both food items were presented simultaneously and the tested animal could only obtain one food item. The rewards were semi-randomly distributed left and right. All animals preferred apple over cucumber in 80% or more ($M = 95\%$) of all choices, and mango over cucumber also in 80% or more ($M = 91\%$) of all choices. We used two different preferred food types, because preference for a reward may decrease when this reward has been obtained frequently (i.e. stimulus satiation) [Hetherington et al., 2002]. The animals had no particular preference for apple over mango or vise versa.

Test Conditions

Subjects and their test partners participated in three different tasks encompassing seven test conditions, depending on the effort required in the equal or unequal reward distribution: no-effort equity,
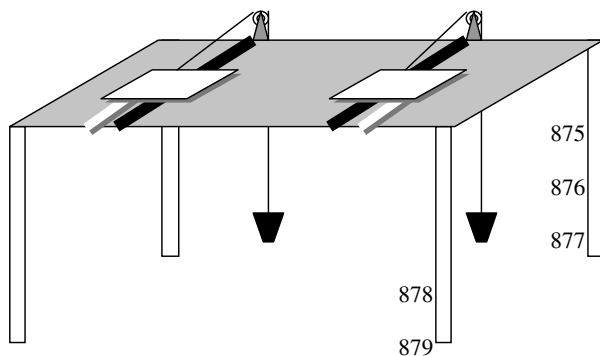

Fig. 1. The test apparatus: The white trays are on top of rails (black bar). In the provisioning conditions, these trays are baited and pushed toward the animals. In the effort conditions, the trays are counterweighted and the monkey has to pull the white handle to get the bait, placed on top of the tray, in range.

TABLE I. Table of the Seven Test Conditions Showing the Rewards Offered to Subject and Partner and the Effort Needed to Pull in the Tray

Condition	Reward subject	Reward partner	Effort subject	Effort partner
1. No effort equity	Cuc.	Cuc.	No	No
2. No effort inequity	Cuc.	Apple	No	No
3. Small effort equity	Cuc.	Cuc.	0.5 kg	0.5 kg
4. Small effort inequity	Cuc.	Apple	0.5 kg	0.5 kg
5. Large effort equity	Cuc.	Cuc.	2.3 kg	2.3 kg
6. Large effort inequity	Cuc.	Mango	2.3 kg	2.3 kg
7. Large effort reward and effort inequity	Cuc.	Mango	2.3 kg	No

Cuc., cucumber.

no-effort inequity, small-effort equity, small-effort inequity, large-effort equity, large-effort inequity, large-effort reward, and effort inequity (Table I). In each condition, the subject and its partner sat side by side in the test chamber. A subject's initial effort level was determined at random, and the equity condition of that effort level was always tested first and followed by the inequity condition 2 days later. Each test session consisted of 20 trials of a single condition for each animal. Each trial was 1 min apart from the previous one. Trials for the subject and its test partner alternated, started with the subject, and the interval between them was half a minute; i.e. trial 1 starts when the subjects gets food on its tray, half a minute later food was placed on the partner's tray, and its first trial starts, again half a minute later the second trial for the subject starts and a new food item is placed on its tray (and the previous one is taken off if the monkey did not take it) and so on. During each condition, both partner and subject remained in the same role (i.e. partner and subject, respectively).

In the "no-effort" conditions, the experimenter pushed a tray with a reward to the subject and to the partner. In the "small-" and "large-effort" conditions, the monkeys had to individually pull in the tray themselves, and this tray was counterweighed with 0.5 and 2.3 kg, respectively. The 0.5 kg was not too hard for the monkeys to pull. However, the 2.3 kg was the maximum weight our smallest individual could reliably pull. The reward distribution between the subject and its partner was either equal: equity or unequal: inequity. The subject was always offered the cucumber, the partner, depending on the condition and the test, was offered cucumber, apple, or mango. In the "large-effort" conditions, an extra condition was added, in which the subject had to pull the heavy weight to obtain the less preferred reward, whereas the partner did not have to pull in the tray itself and the experimenter pushed the tray with the more preferred reward to it, thus creating both reward and effort inequity (Table I).

Measures

As a measure of willingness to participate in the test, we scored whether an animal took the reward in the provisioning conditions and whether the animal successfully pulled in the tray and then took the reward in those conditions where an effort was needed [Brosnan & de Waal, 2003; Brosnan et al., 2005]. All animals always took the reward after having pulled in the tray in those conditions where an effort was needed. For the sake of brevity, in the remainder of this article we, therefore, refer to the proportion of rewards taken as a measure of willingness in both the conditions were an effort was needed and in which the animals were provisioned. A refusal to accept the reward was defined as a trial in which the subject did not take the reward within 60 sec in the provisioning conditions. A refusal to conduct the task was defined as a trial in which the subject did not pull in the tray and take the reward within 60 sec. A stopwatch was used to determine the beginning and ending of a trial, and thus whether the reward would be taken back after the subject refused to accept or conduct the task within the 60 sec. The delay in conducting the task or taking the reward was defined as the time it took the subject to conduct the task or take the reward (between 0 and 60 sec) after the reward was placed on the tray.

To test for IA, we compared these measures between the equity and inequity conditions within the separate tasks with different effort levels (no effort, small effort, and large effort). In addition, we measured all affiliative (i.e. lip smacking and eye lifting) and aggressive (i.e. open mouth threats, "pointing," and serial grunts) behavior [Angst, 1974] of the subjects toward their partners and vice versa to test for frustration owing to inequity. However, we did not see any such behavior during either inequity or equity conditions and, therefore, performed no tests on these behaviors. Moreover, results (and statistics) of the analyses of the latencies were usually not significant, but were usually longer in conditions where subjects or partners were less likely to accept the reward and are for reasons of brevity only provided in the supplemental materials.

In addition, subjects may not immediately recognize the fact that reward distributions are unequal in the inequity conditions, but learn over time [Brosnan & de Waal, 2003]. Therefore, we also compared between equity and inequity conditions

the proportion of rewards taken by the subject in the last eight trials. The results (and statistics) of the analyses of only the last eight trials were similar to those of the proportions of rewards taken. For reasons of brevity, these are only provided in the supplemental materials.

Moreover, to test the effect of several variables on IA, we calculated an inequity response. The inequity response is defined as the proportion of rewards taken by the subject in the inequity condition minus the proportion of rewards taken by the subject in the equity condition.

All test sessions were recorded using a Sharp VL-E610 video 8 recorder (Sharp VL-E610, Houten, The Netherlands) and data were coded by J.J.M.M. Coding could not be blind because subjects, their behavior, and conditions were visible. Fifteen percent of all tapes were recoded by L.M.v/d.B. Interobserver reliability was calculated using Cohen's for the proportion of rewards taken and a Pearson's correlation for the latencies. Both proportion of rewards taken and latencies were scored almost perfectly similar (= 0.995 and Spearman's correlation coefficient = 0.996, $N = 840$, $P < 0.0001$).

Data Analysis

Our data were not normally distributed; therefore, we used nonparametric tests. Because the pairs of subject and their partner in both experiments remained the same in all conditions, we used paired sample comparisons. When Wilcoxon signed ranks tests were applied, we showed the sum of positive ranks and the exact P-values [Mundry & Fischer, 1998]. In this study, $\alpha = 0.05$ and tests were two-tailed.

RESULTS

Evaluating Own Effort and Reward

We first tested whether the long-tailed macaques pay attention to their own effort and reward. Therefore, we compared the proportion of rewards taken by all animals (both subjects and partners) in the equity conditions of the three different effort levels using a Friedman's test. We found an overall difference in the proportion of rewards taken ($N = 19$, $\chi^2 = 15.84$, $df = 2$, $P = 0.001$) (Fig. 2). Post hoc analysis using Wilcoxon signed ranks tests showed a significant drop ($ES = 0.82$) in the proportion of rewards taken between no effort ($M = 0.74$, $SE = 0.07$) and large effort ($M = 0.41$, $SE = 0.08$; $N = 19$, $T^+ = 152$, $P < 0.001$), and a significant drop ($ES = 0.59$) in the proportion of rewards taken between small effort ($M = 0.65$, $SE = 0.09$) and large effort ($N = 19$, $T^+ = 117.5$, $P = 0.008$). There was no significant difference in proportion of rewards taken between no effort and small effort ($N = 19$, $T^+ = 62.5$, $P = 0.115$) (Fig. 2).
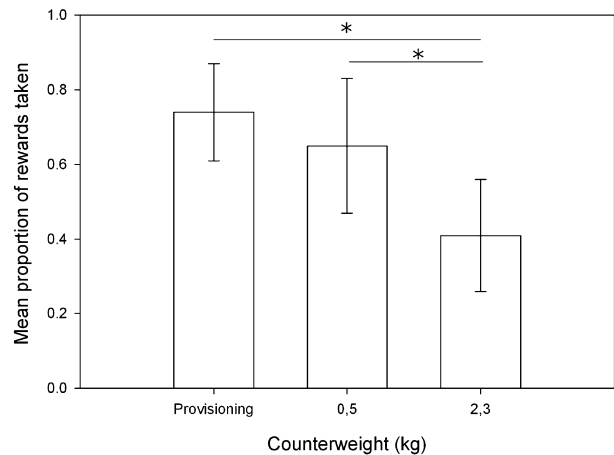

Fig. 2. Mean proportion of rewards taken by all animals (both subjects and partners) in the equity conditions when provisioned, with small effort (pulling in a counterweight of 0.5 kg) and with large effort (pulling in a counterweight of 2.3 kg), with 95% confidence intervals plotted. $^{*}P < 0.05$.
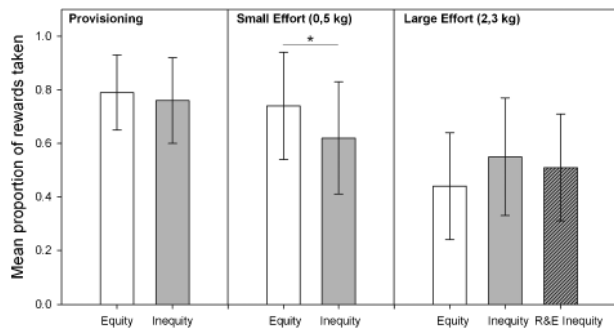

Fig. 3. Mean proportion of rewards taken by dominant subjects in the equity (white bars), inequity (grey bars), and reward and effort inequity (striped bars) conditions when provisioned, with small effort (pulling in a counterweight of 0.5 kg) and with large effort (pulling in a counterweight of 2.3 kg), with 95% confidence intervals plotted. $^{*}P < 0.05$.

Inequity Aversion

To test for IA, we compared the proportion of rewards taken by the subjects in the equity condition with the proportion of rewards taken in the inequity condition for the three effort levels separately, using Wilcoxon signed ranks tests (Fig. 3). When the subjects were provisioned, we found no significant difference in the proportion of rewards taken by the subjects between the equity ($M = 0.79$, $SE = 0.07$) and inequity ($M = 0.76$, $SE = 0.08$) condition ($N = 12$, $T^+ = 21$, $P = 0.719$). In the small-effort conditions, however, we did find a significant difference ($ES = 0.65$) in the proportion of rewards taken between the equity ($M = 0.74$, $SE = 0.10$) and inequity ($M = 0.62$, $SE = 0.11$) condition ($N = 12$, $T^+ = 34$, $P = 0.023$). The subjects took significantly fewer rewards when their partners received a more preferred reward for the same effort. In the large-effort conditions, however, we found no significant difference in the proportion of rewards

taken between the equity ($M = 0.44$, $SE = 0.10$) and inequity ($M = 0.55$, $SE = 0.11$) condition ($N = 12$, $T^+ = 8.5$, $P = 0.211$). Moreover, no significant difference was found in the proportion of rewards taken between the equity ($M = 0.44$, $SE = 0.10$) and reward and effort inequity ($M = 0.51$, $SE = 0.10$) condition ($N = 12$, $T^+ = 15.5$, $P = 0.250$) (Fig. 3). Altogether, long-tailed macaques showed IA, however, only in the small-effort condition.

Advantageous Inequity Aversion: To test for advantageous IA in the subordinate partners, we compared the proportion of rewards taken by these subordinate partners in the equity conditions with the proportion of rewards taken in the inequity conditions, using Wilcoxon signed ranks tests (Fig. 4). We found no significant difference in the proportion of rewards taken between equity and inequity conditions when the subordinate partners were provisioned (equity: $M = 0.66$, $SE = 0.13$; inequity: $M = 0.79$, $SE = 0.11$) or when only a small effort was required to perform the task (equity: $M = 0.52$, $SE = 0.14$; inequity: $M = 0.66$, $SE = 0.12$; no effort: $N = 9$, $T^+ = 3$, $P = 0.156$; small effort: $N = 9$, $T^+ = 4$, $P = 0.219$). In the large-effort conditions, subordinate partners took significantly ($ES = 0.84$) more rewards when they received the more preferred reward in the inequity condition ($M = 0.69$, $SE = 0.11$) than when they received the less preferred reward in the equity condition ($M = 0.37$, $SE = 0.12$; $N = 9$, $T^+ = 0$, $P = 0.008$). A similar trend ($ES = 0.65$) was found between the reward and effort inequity condition ($M = 0.63$, $SE = 0.12$) and the equity condition in the large-effort conditions ($N = 9$, $T^+ = 4$, $P = 0.055$) (Fig. 4). Altogether, we have no evidence for advantageous IA in long-tailed macaques.

Rank and RQ Effects

Further analyses of the inequity response of the dominant subjects in the small-effort conditions, using Spearman's rank correlations, revealed no
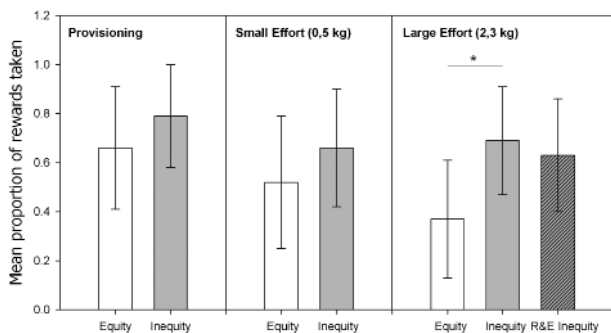

Fig. 4. Mean proportion of rewards taken by subordinate partners in the equity (white bars), inequity (grey bars), and reward and effort inequity (striped bars) conditions when provisioned, with small effort (pulling in a counterweight of 0.5 kg) and with large effort (pulling in a counterweight of 2.3 kg), with 95% confidence intervals plotted. *$P < 0.05$.

significant effect of subject's rank ($\rho = 0.152$, $N = 14$, $P = 0.603$), the pair's rank difference ($\rho = 0.077$, $n = 14$, $P = 0.794$), or the pair's RQ ($\rho = -0.180$, $N = 14$, $P = 0.538$) on this response.

DISCUSSION EXPERIMENT 1

Our results show that long-tailed macaques work less for the same reward when workload increases, and at high workload work more for a more preferred reward. This indicates that long-tailed macaques pay attention to the pay-off of their own effort and reward, as is found in many mammals [Cooper & Mason, 2001]. This is a prerequisite necessary for IA. Moreover, our results show that in the small-effort conditions the subjects exhibit IA. In contrast, they do not show IA when provisioned. This supports the argument of van Wolkenten et al. [2007] that an effort to obtain a reward is required to find IA.

In the large-effort conditions, however, the long-tailed macaques showed no IA. This result may indicate that the IA found in the small-effort condition is owing to a type I error. Alternatively, the lack of IA in the large-effort condition may result from the general low proportion of rewards taken in the large-effort conditions and from the animals aiming to obtain at least a minimum amount of rewards in a test, irrespective of what their partner gets.

Original findings on IA in animals have been attributed to frustration of subjects owing to receiving a less preferred reward, after having received the more preferred reward for the same task [Roma et al., 2006; Silberberg et al., 2009]. However, our results cannot be explained by this frustration effect, because, apart from the two subjects that were used as both subject and partner, none of the subjects ever received the more preferred reward for performing the task. Omitting the results of those two subjects that were used as both subject and partner still gives a significant difference between the equity and inequity condition with small effort (Wilcoxon signed ranks test; $N = 10$, $T^+ = 26$, $P = 0.047$).

We expected an effect of rank difference and RQ on the response to inequity. However, we did not find such effects. Because the design of the study was to find IA, and we only tested dominant individuals with nonfriend partners, variation in both rank relationship and RQ were rather low and, therefore, possible effects may have been obscured. To test the effect of RQ in more detail, we designed a second experiment.

EXPERIMENT 2: FRIENDSHIP AND IA IN LONG-TAILED MACAQUES

Because friends are expected to distribute resources according to differences in need instead

of equitable distributions [Clark & Mills, 1979; Deutsch, 1975], it is expected that friends are more tolerant to inequity than nonfriends. To determine this, we tested subjects with both a friend and a nonfriend partner. In this experiment, we used the same small-effort conditions as in experiment 1, because in this condition the dominant individuals expressed IA. Hence, individuals had to work a little to obtain a reward, as did their partners. Partners received either a similar (equity condition) or a more preferred (inequity condition) reward.

METHODS

Subjects

The study subjects for experiment 2 were drawn from the same social group as the ones in experiment 1. We selected 13 individuals and paired them with both a nonkin friend and a nonkin nonfriend, yielding 6 male and 7 female subjects with same-sex friends and nonfriends. The friend dyads had a mean rank difference of 5.0 ($\sigma = 9.2$) and the nonfriends dyads had a mean rank difference of 8.3 ($\sigma = 7.7$) (for a table of the dyads, see supplemental materials).

The data for friendship status and dominance hierarchy were the same as in experiment 1.

Test Conditions

Test environment, apparatus, and measures were the same as in experiment 1. As in experiment 1, in each condition the subject and its partner sat side by side in the test chamber. Whether a subject was tested first with its friend or nonfriend was counterbalanced. The complete test with the first partner was first finished before testing the individual with its other partner. In each dyad, the equity condition was always tested first. To control frustration owing to not receiving the visible more preferred reward (i.e. a violation of expected rewards, in contrast to a violation of expected reward distribution, i.e. IA) [Bräuer et al., 2006; Dubreuil et al., 2006], the preferred reward was always visible in both the equity and the inequity condition. Each test session consisted of 20 trials of a single condition for each animal. Each trial was a minute apart from the previous one. Trials alternated between partner and subject, and we always started with the partner. However, during each condition, both partner and subject remained in the same role (i.e. partner and subject, respectively). Subjects and test partners were never tested more than once on the same day and there was always at least one day between two conditions for both subjects and test partners.

RESULTS

Inequity Aversion

First, we tested whether we could reproduce the results from experiment 1, using a Wilcoxon signed ranks test. Although we now controlled frustration simply owing to not receiving a visible yet more preferred reward (the preferred reward was always visible), we again found that the long-tailed macaques show IA. The mean proportion of rewards taken by the subject was significantly ($ES = 0.57$) lower in the inequity conditions ($M = 0.64$, $SE = 0.08$) compared with the equity conditions ($M = 0.72$, $SE = 0.08$; $N = 13$, $T^+ = 56$, $P = 0.038$) (Fig. 5).

Alternative Explanations

To test whether the inequity response in the small-effort condition of experiment 1 was owing to frustration of the subjects caused by not receiving the visible yet more preferred reward rather than to a violation of expected reward distribution (i.e. IA), we compared the proportion of rewards taken in the equity conditions by those animals that were subject in both experiments. In experiment 2, in the equity condition, the more preferred reward was always visible, whereas this was not the case in this condition in experiment 1. When a reaction to not receiving the visible yet more preferred reward is present, this will result in a lower proportion of rewards taken in experiment 2 than in experiment 1. However, using a Wilcoxon signed ranks test, we did not find a significant difference in the proportion of rewards taken by those animals in the equity conditions with small effort in experiment 1 ($M = 0.71$, $SE = 0.11$) and the equity condition with small effort in experiment 2 ($M = 0.71$, $SE = 0.09$; $N = 11$, $T^+ = 16$, $P = 0.844$). It could be argued that order effects may confound this test, yet if there would be an effect of test order, we would expect that subjects would pull less in experiment 2 than experiment 1 owing to habituation effects. Thus, if we would have found a significant difference of pulling less during experiment 2 than experiment 1, this may have been owing to either frustration or habituation. However, because we did not find such
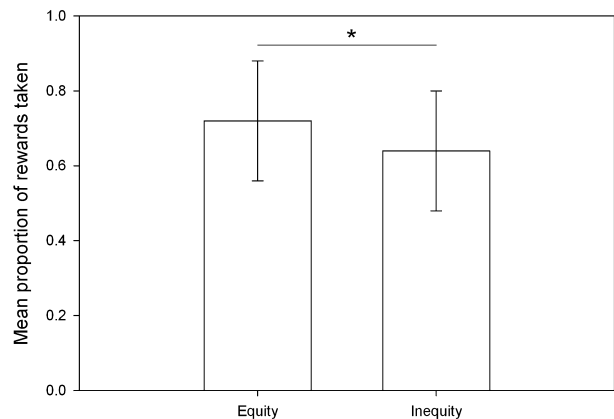

Fig. 5. Mean proportion of rewards taken by the subjects in the equity and inequity conditions, with 95% confidence intervals plotted. *$P < 0.05$.

an effect, we interpret this that neither was responsible for the results.

Inequity Aversion and Friendship

The effect of RQ on IA was determined by testing whether the response to inequity (i.e. the proportion of rewards taken in the inequity condition–the proportion of rewards taken in the equity condition) differs when subjects were paired with a friend compared with when paired with a nonfriend, using a Wilcoxon signed ranks test. However, no significant difference in inequity response was found between friends ($M = -0.16$, $SE = 0.08$) and nonfriends ($M = -0.07$, $SE = 0.05$; $N = 13$, $T^+ = 29.5$, $P = 0.445$) (Fig. 6).

DISCUSSION EXPERIMENT 2

The results of experiment 2 show IA when a moderate effort is required in long-tailed macaques. Furthermore, we show that this effect cannot be explained by frustration of the subjects owing to simply not receiving a visible, yet more preferred reward [Bräuer et al., 2006; Dubreuil et al., 2006], because we controlled for that. In addition, the results of experiment 2 show that the inequity response measured in experiment 1 also cannot be explained by this frustration effect.

Our results show no difference in inequity response between friend and nonfriend dyads. Apart from the absence of an effect of RQ on the inequity response, this result may also be explained by a lack of intentionality of the friend [Falk et al., 2008; Rabin, 1993], because it was the experimenter and not the partner that was responsible for the unequal distribution of the rewards. Alternatively, as the chimpanzees in the experiment of Brosnan et al. [2005], these long-tailed macaques have resided in a stable social group for a long period, and RQ in general may be high and variation herein low.
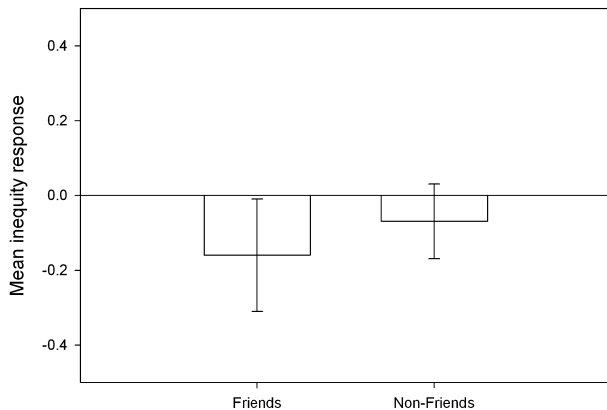

Fig. 6. Mean inequity response (calculated as: prop. of rewards taken in the inequity condition–prop. of rewards taken in the equity condition) of the subjects with friend and nonfriend partner, with 95% confidence intervals plotted.

GENERAL DISCUSSION

IA in Long-Tailed Macaques

We hypothesized that dominant long-tailed macaques will show IA when treated unequally, because it contrasts with the distribution of preferred food items in their everyday lives [Sterck et al, 1997; van Schaik, 1989]. IA consists of two parts: first, the evaluation of one's own pay-off and, second, the comparison of this evaluation with the pay-off of another individual. We determined whether long-tailed macaques exhibited both capacities. Long-tailed macaques evaluated their own costs and benefits, similar to many other mammals [Cooper & Mason, 2001]. With increasing effort needed, the rate of refusals to perform the task for the same reward also increased. Moreover, long-tailed macaques perform the task more often when the reward is more preferred if a large effort was needed to perform the task. Therefore, we conclude that long-tailed macaques comply with the first condition of IA.

In addition, dominant long-tailed macaques comply with the second condition and can show IA when their partner obtains a more preferred food item. However, in the first experiment, the animals only showed IA in one out of four different inequity manipulations, suggesting that this may be owing to a type I error. Yet, because we could replicate this result in the second experiment and given the large effect sizes in both experiments, we think this is highly unlikely. Therefore, we conclude that dominant long-tailed macaques can show IA.

The original findings of IA [Brosnan & de Waal, 2003; Brosnan et al., 2005] have been attributed to either a frustration effects owing to receiving a less preferred reward than in a previous trial [Roma et al., 2006; Silberberg et al., 2009] or frustration owing to not receiving a visible yet more preferred reward [Bräuer et al., 2006; Dubreuil et al., 2006]. We controlled both phenomena in the design of our study and still found IA. Therefore, IA in long-tailed macaques cannot be explained by either effect. Moreover, we tested whether the visibility of a more preferred reward actually affected long-tailed macaques' behavior, and found no change in their acceptance of rewards. Also, capuchin monkeys do not show a reaction to a visible yet more preferred rewards [van Wolkenten et al., 2007], but it has been found in cotton-top tamarins [Neiworth et al., 2009]. Nonetheless, cotton-top tamarins showed IA after controlling for this frustration effect. Therefore, the proposed alternative explanations cannot explain the IA found in long-tailed macaques and other species.

IA and Effort

Our results indicate that IA in long-tailed macaques is only shown under certain circumstances: an effort to obtain the reward is crucial for

finding IA, because long-tailed macaques do not show IA when they are provisioned and no effort is required. This is similar to capuchin monkey studies that required an effort from their subjects [Brosnan & de Waal, 2006; Brosnan et al., 2010; van Wolkenten et al., 2007] and counters the claim of absence of IA in studies that did not require an effort from their subjects [Dubreuil et al., 2006; Roma et al., 2006; Silberberg et al., 2009]. Therefore, our results confirm that some effort is a crucial factor for IA.

However, when a large effort was required, we did not find IA. This contrasts with studies that find a larger IA effect when the effort increases [van Wolkenten et al., 2007]. However, in contrast to the bartering paradigm normally used in this line of research, our task required the monkeys to pull a very heavy load; for some, even the maximum weight they could pull. This large effort may have changed their assessment of the task. We argued that an IA task consists of two components, i.e. the amount of reward relative to the effort and the IA part. In addition, animals may aim to obtain a minimum amount of rewards in a test, irrespective of the IA condition. Therefore, when the level of the minimum amount of rewards is reached owing to the large decrease of rewards taken caused by a large effort, no effect of IA will be measured. In support of this argument that animals maintain a minimum reward is the finding that subjects still obtain rewards in IA tasks, although at lower levels [Brosnan & de Waal, 2006; Brosnan et al., 2005; Neiworth et al., 2009; Range et al., 2009a; van Wolkenten et al., 2007]. In addition, an effect of the cost–benefit ratio on performance has been found in tasks where animals had to wait for extensive periods, and they only perform in a limited number of the tasks, e.g. chimpanzees [Dufour et al., 2007] and long-tailed macaques [Pelé et al., 2010]. A similar bottom-line performance may have determined the amount of pulling in our large-effort task. This implies that studies on IA did find that a larger effort enhances IA, where the monkeys had to exchange tokens more often [Brosnan et al., 2010; Neiworth et al., 2009; van Wolkenten et al., 2007], did not ask a maximum performance of the tested animals. Consequently, how effort relates to IA at high-effort levels remains to be investigated further.

IA and Domain Specificity

IA in animals has been tested using a food paradigm. Thus far, IA was only tested in species that also cooperate in the food domain. When IA is domain specific, IA will only be found in these species and not in species that do not share food or cooperate to obtain food. Our study employed a similar food paradigm and showed IA in a species that does not cooperate in the food domain, yet does cooperate in the social domain (e.g. coalitionary support) [de Waal, 1977; van Noordwijk & van Schaik, 1985]. That these animals also react to an unequal distribution of food suggests that IA is not domain specific and that IA is a higher order capacity that they can employ in several contexts [Brosnan, 2011; see also Talbot et al., 2011].

IA and relationship characteristics: We hypothesized an effect of the social organization of long-tailed macaques on the expression of IA [cf. Bräuer et al., 2006, 2009; Brosnan et al., 2010]. We proposed that only dominants would express IA when paired with a subordinate and that subordinates would not when paired with a dominant. In accordance with previous studies [Bräuer et al., 2006, 2009; Brosnan et al., 2010], we did find in this study that dominants express IA, but we only tested dominant individuals and thus did not test the second part of our hypothesis.

Furthermore, we expected an effect of RQ on the expression of IA. A relation between IA and RQ is suggested in the human literature [Clark & Mills, 1979], yet was, to our knowledge, never formally tested in nonhuman animals. Post hoc analyses, however, did show that social closeness in chimpanzees may inhibit the expression of IA [Brosnan et al., 2005] and that more tolerant dogs also expressed less IA [Range et al., 2009b]. In this study, we designed our second experiment to test subjects with a friend and a nonfriend. Nevertheless, we did not find a difference in the expression of IA of individuals paired with their friend or a nonfriend. However, the variation of RQ in a captive group may be rather small, because all individuals interact frequently with each other and there are no strangers. Therefore, our result does not preclude that an effect of RQ on IA exists in other species or in long-tailed macaques for other relationships. Therefore, it would be of great interest to determine what the effect of, for example, kinship on IA may be, especially in light of kin selection theory [Hamilton, 1964].

Evolution of IA

Researchers have suggested that IA is a specialized and advanced social capacity that will only be found in a limited number of species. It has been proposed that capuchin monkeys evolved such specialized and advanced social capacities because of their extensive use of tools and cooperative hunting skills [Neiworth et al., 2009; Parker & McKinney, 1999]. Similarly, these skills may account for the evolution of IA in chimpanzees. However, neither long-tailed macaques nor cotton-top tamarins habitually use tools or cooperatively hunt, but do show IA. Consequently, the evolution of IA is not uniquely linked to these skills. Alternatively, it has been suggested that assessment of inequity is a trait

shared among those primates that are socially tolerant [Neiworth et al., 2009]. Because long-tailed macaques are not considered socially tolerant [Thierry, 2000], we suggest that IA does not depend on social attitude either.

The species that show IA are from several Anthropoid primate taxa: IA is found in apes, i.e. chimpanzees [Brosnan et al., 2005], New World monkeys, i.e. brown capuchins and cotton-top tamarins [Brosnan & de Waal, 2003; Neiworth et al., 2009], and Old World monkeys (this study). Moreover, neither specialized skills nor social attitude seem to determine the presence of IA. However, IA may be limited to primate species that cooperate [Brosnan, 2011], because it has not been shown in primate species that do not habitually cooperate, i.e. orangutans and squirrel monkeys [Brosnan et al., 2011; Talbot et al., 2011]. Apart from several species, cooperation is probably a widespread capacity among Anthropoid primates, yet the context in which it is used may differ (e.g. female support of kin to obtain rank: long-tailed macaques [van Noordwijk & van Schaik, 1987]; female aggression against infanticidal males: Hanuman langurs, *Semnopithecus* sp. [Hrdy, 1977]). Therefore, we predict that IA is present in all Anthropoid primates that do habitually cooperate in any context.

We conclude that long-tailed macaques can express IA when treated unequally and that some effort to obtain the reward is crucial for the occurrence of this behavior; yet, a large effort may obscure it. Although we aimed to determine whether relationship characteristics affected IA, we did not find such an effect for ''friends,'' but suggest IA may depend on the dominance relationship. Furthermore, IA seems a primate trait that is not domain specific and present in all Anthropoid primates that habitually cooperate, independent of social organization. Therefore, IA may be a social tool that these primate species can employ in different contexts. Future research should focus on the social conditions that facilitate the use of IA animals.

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