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Aversion to violation of expectations of food distribution: the role of social tolerance and relative dominance in seven primate species

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Abstract

Studies on how animals behave when two partners receive different amounts of food have produced variable results, with individuals responding negatively to specific food distributions in some cases (e.g., when food is distributed unequally between partners), but not in others. In this study, we used a simple experimental approach to (i) assess the strictness of dominance relationships based on the degree of social tolerance and (ii) compare the behavioural responses of seven primate species (chimpanzees, *Pan troglodytes*; bonobos, *Pan paniscus*; gorillas, *Gorilla gorilla*; orangutans, *Pongo pygmaeus*; brown capuchin monkeys, *Cebus apella*; spider monkeys, *Ateles geoffroyi*; long-tailed macaques, *Macaca fascicularis*), when two partners received different amounts of food and no effort was required. We predicted that negative responses (i.e., refusal to participate in the task or avoidance of proximity to the food source) would be elicited by food distributions that violate the individual expectations based on tolerance levels and subject's dominance rank relative to the partner. In the 'tolerance' task, we found that species with less strict dominance relationships were chimpanzees and bonobos, followed by orangutans, spider monkeys, gorillas, brown capuchin monkeys and long-tailed macaques. In the 'food distribution' task, capuchin monkeys and especially macaques showed their aversion by refusing to participate in most conditions, including the ones with equal food distribution. When dominants received more food than the partner, subjects of all species maintained a comparable amount of proximity to the food source,

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possibly reflecting the general acceptance of such a food distribution across species. When dominants received less than or as much as their partners, dominant capuchin monkeys maintained less proximity than other species, possibly because having different expectations of food distributions (i.e., more/all food to the dominant). Our study highlights the importance of the species' degree of social tolerance and the relative dominance rank between partners in the study of violation of expectations of different food distributions.

Keywords
social tolerance, comparative cognition, great apes, spider monkeys, capuchin monkeys, long-tailed macaques.

1. Introduction

In the last decade, much research effort has been devoted to study how animals behave when two individuals are presented with different amounts of food. Typically, these studies have investigated whether individuals respond negatively to receiving an outcome differing from that of their partners by refusing to accept the reward or by stopping to participate in the test. Responding in such a manner to a disadvantageous reward distribution might increase individuals' relative fitness as compared with individuals who do not, if repeated opportunities for interaction are available in the long term (Brosnan & de Waal, 2004; Brosnan et al., 2011). Although rejecting unequal food distributions goes against the assumptions of traditional economics, because fitness maximization implies individuals to take whatever they are given regardless of what their partners are given, in the long term, showing aversion to food distributions that violate expectations would indeed keep individuals from being taken advantage of (de Waal, 2006).

Most experimental studies on responses to food distribution have focused on inequity aversion, i.e., on how individuals resist inequitable outcomes (Fehr & Schmidt, 1999). In these studies, subjects typically have to make an effort to receive less valuable food (LVF) in exchange for tokens, but their partners are either given the same LVF or a more valuable food (MVF; e.g., Brosnan & de Waal, 2003). With this procedure, subjects appear to be less likely to exchange a token for LVF when the partner is given MVF, possibly as a result of comparing their own rewards with those of others and refusing to complete interactions when conditions are perceived as unfair (Brosnan & de Waal, 2003, 2006). Although other studies have produced different results and their interpretations are not univocal (e.g., Braeuer et al., 2006, 2009; Silberberg et al., 2009), evidence is being gathered that subjects' effort to obtain food is necessary (although not sufficient) to solicit subjects' aversion to unequal food distributions (e.g., Brosnan & de Waal, 2006; Dindo & de Waal, 2007; van Wolkenten et al., 2007; Neiworth et al., 2009; Brosnan et al., 2010; Takimoto & Fujita, 2011; Massen et al., 2012). When effort is required, primates appear to perceive the events differently from when no effort is required. Whereas receiving food after some effort may induce a comparison of benefits and costs among partners (and create aversion to unfair food distributions), receiving food at no cost may resemble normal feeding situations, in which food is often unequally distributed among partners (Dindo & de Waal, 2007; van Wolketen et al., 2007; Talbot et al., 2011).

Consequently, aversion to specific food distributions has also been investigated when two subjects receive different amounts of food and no effort (e.g., token exchange) is required. In this situation, capuchin monkeys and great apes who receive LVF spend more time in proximity to the food source and show less aversion when the partner is given MVF than when there is no partner or the partner is also given LVF (Braeuer et al., 2006; Dindo & de Waal, 2006; Dubreuil et al., 2006). In contrast to the change in behaviour seen in these studies, others have found that individuals do not respond differently to unequal food distributions when no effort is required, although they may when effort is included (e.g., chimpanzees: Brosnan et al., 2010; squirrel monkeys: Talbot et al., 2011; see also Neiworth et al., 2009, on cotton-top tamarins). Surprisingly, most of these studies do not analyse separately the behaviour of the dominant and subordinate subjects, although some of them have evidenced important differences between dominants and subordinates in terms of their aversion to food distributions (e.g., Braeuer et al., 2006 on great apes; Brosnan et al., 2010 on chimpanzees; Massen et al., 2012 on long-tailed macaques; but see Takimoto & Fujita, 2011 on capuchin monkeys). In great apes, for example, dominants show more aversion than subordinates when partners receive MVF, possibly because they are not used to receive LVF during every-day competitive interactions with other partners (Braeuer et al., 2006).

In this respect, de Waal (1996) crucially proposed that primates might develop a set of expectations about the way in which they should be treated and how resources should be divided. Deviations from these expectations would lead to negative responses, like subordinates avoiding proximity to the food source or refusing food, and dominants being aggressive. The strictness of dominance relationships based on the degree of social tolerance could influence a species' expectations and, therefore, when and how subjects negatively respond to outcomes that are perceived as unexpected. Therefore, in more despotic species subordinates do not expect to receive anything from more dominant partners, whereas in more tolerant species subordinates usually receive some share of resources or can protest against dominants without much fear of retribution, so that their expectations about distribution of food resources might be more equitable than in more despotic species (de Waal, 1996, 2006; Brosnan, 2006). For example, species characterized by higher levels of social tolerance, like bonobos, should have more equitable expectations of food distributions (Hare et al., 2007; Braeuer et al., 2009). However, no systematic comparative studies have so far been conducted to support this hypothesis.

The aim of the present study was, therefore, to examine the effect of species' strictness of dominance relationships in the responses to different food distributions between partners in seven primate species: chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*), brown capuchin monkeys (*Cebus apella*), spider monkeys (*Ateles geoffroyi*) and long-tailed macaques (*Macaca fascicularis*). For this purpose, we experimentally assessed the degree of strictness of dominance relationships in each species by testing the degree of social tolerance between two individuals when juice was made accessible to both of them. Then, we tested for inter-specific differences in individuals' responses when their partners in a dyad received different amounts of food. Considering the discrepancy in the results so far obtained (see above), the design of our task was maintained as simple as possible to avoid introducing possible confounding factors in terms of inter-specific differences in the cognitive abilities required to understand the task. We used different quantities of food when distributing food to the subject, and not different types of food, in order to avoid that the magnitude of food preferences, which might not be universal across species, may mask inter-specific differences (e.g., Brosnan & de Waal, 2006; Roma et al., 2006).

If expectations of food distribution differ across species depending on the strictness of dominance relationships and negative responses are elicited by distributions that violate these expectations, dominant subjects are predicted to show aversion whenever receiving less than expected (i.e., dominants expecting much more food in highly despotic species and slightly more or the same amount of food as subordinates in more tolerant species). Subordinate subjects instead are expected to show aversion when receiving more than expected out of fear of retaliation from dominant partners, with subordinates in more despotic species presumably expecting to receive much less and subordinates in more tolerant species expecting to receive slightly less or the same amount of food as dominants. Thus, the comparative approach used in this study together with the data we collected on social tolerance allowed us to interpret inter-specific differences in response to different food distributions within the socio-ecological context of species expectations.

2. Material and methods

2.1. Subjects

We tested 7 spider monkeys at the Centenario Zoo in Merida, Mexico, 7 brown capuchin monkeys at the ISTC-CNR Primate Centre in Rome, Italy, 7 long-tailed macaques at the Research Group Behavioral Biology, University of Utrecht, Netherlands, and 11 chimpanzees, 5 bonobos, 5 orangutans and 5 gorillas at the Wolfgang Koehler Primate Research Center in the Leipzig Zoo, Germany. Subjects were of both sexes and various ages (classified as adults, subadults and juveniles according to Smuts et al., 1987; Kappeler & Pereira, 2003), and they were all born in captivity, except for the spider monkeys, who were born in the wild but were raised as pets before being rescued and brought to the zoo (Table 1). Subjects were all housed in groups with their conspecifics, in enclosures with outdoor and indoor areas, and they were never deprived of food or water before or during the experiment. All of the subjects were previously used to being temporally isolated in testing rooms and were tested by the same familiar experimenter only after they were comfortable with the set-up and the testing room. All subjects had previously participated in experimental tasks, but none of them had been previously tested in the same tasks administered in this study (21 great apes and 1 capuchin monkey had been tested on a similar task by Braeuer et al., 2006 and Dubreuil et al., 2006 respectively; see Table 1 for more details).

The relative dominance between individuals in each tested dyad was determined shortly before this study. For spider monkeys, capuchin monkeys and long-tailed macaques, we recorded the outcome of food competition tasks (i.e., the experimenter threw one piece of food in between the two individuals when they were equally attentive and no other individual was in the area, recording which individual obtained the food). At least 6 tasks were

Table 1.
Age and sex of the tested subjects.

Subject	Species	Sex	Age
1	Spider monkey	F	S
2		F	S
3		M	S
4		M	S
7		F	A
8		F	A
11		F	A
Cognac	Capuchin monkey	M	A
Paquita		F	A
Pedro		M	S
Penelope		F	S
Robin Hood*		M	A
Rubens		M	S
Rucola		F	S
Anastasia	Long-tailed macaque	F	J
Cleo		M	A
Era		F	A
Icetea		F	A
Linea		F	S
Salvadoro		M	J
Video		M	S
Alex	Chimpanzee	M	S
Alexandra		F	S
Annett		F	S
Dorien*		F	A
Fifi*		F	A
Frodo*		M	A
Jahaga*		F	A
Riet*		F	A
Sandra*		F	A
Trudi*		F	A
Unyorio		M	A
Joey*	Bonobo	M	A
Kuno*		M	A
Limbuko*		M	A
Ulindi*		F	A
Yasa		F	A

Table 1.
(Continued.)

Subject	Species	Sex	Age
Bimbo*	Orangutan	M	A
Dokana*		F	A
Dunja*		F	A
Padana*		F	A
Pini*		F	A
Bebe*	Gorilla	F	A
Gorgo*		M	A
N'diki*		F	A
Ruby*		F	A
Viringika*		F	A

Sex (M, male; F, female); age class (A, adult; S, subadult; J, juvenile; according to the literature: Smuts et al., 1986; Kappeler & Pereira, 2003).

* Subject had been already tested with a similar paradigm (great apes: Braeuer et al., 2006; capuchin monkeys: Dubreuil et al., 2006).

carried out for each dyad (mean: 9), and the individual obtaining the food most of the times was considered as dominant within the dyad. For the great apes, the keepers working at the facility discussed and agreed on the relative dominance of the individuals in each dyad based on the outcome of agonistic interactions, submissive behaviours and order of access to food resources they witnessed. In this study the terms dominant and subordinate, therefore, refer to the relative dominance between the two individuals in each tested dyad.

2.2. Materials and procedure

Two subjects were positioned in the testing room. For great apes (and one dyad of spider monkeys for logistic reasons), one single mesh partitioned the testing room in two similar parts, where subjects were separately housed throughout the test but with constant visual and physical access to each other through the bars. In this case, the two parts of the testing room were always adjacent, so that the subjects could always be in direct visual and physical contact. For the three monkey species, subjects were together in the testing room. In the tolerance task, subjects were first habituated to drink juice from transparent plastic drinkers when alone. During the task, each dyad was separately tested in the testing room, where two drinkers had been previously arranged at a distance of 0.5 m (close condition) or 1.00 m from each other (far condition). Trials were ended after 2 min or when one of the drinkers was empty (the fact that trials rarely lasted less than 2 min had no effect on our results, as tolerance values were measured in terms of the proportion of time each subject spent simultaneously drinking with the partner out of the total time spent drinking; see below). Each dyad underwent only one trial for the close condition and on a subsequent day one trial for the far condition.

In the food distribution task, the experimenter sat in front of the testing room, in-between the two subjects, with food clearly visible to minimize the inhibitory effect that preoccupation with obtaining rewards might exert on subjects' performance (Warneken & Tomasello, 2006; Warneken et al., 2007). Food could only be accessed if the subject got close to the experimenter when the experimenter stretched out her arm in the subject's direction, close to the bars that separated subjects and experimenter (i.e., subjects had to be one arm length from each other to receive food). Food consisted of raisins or commercial primate pellets, according to the species' preferences and their diet prescriptions. Different quantities of the same food (1 versus 3), instead of different types of food, were used to be sure that MVF was always preferred to LVF in all dyads and species (cf., Brosnan & de Waal, 2006). All tested species consistently prefer the larger quantity of food to the smaller one, as reported in other studies confronting the same sets of subjects with different amounts of food (delay of gratification task using 1:3 pieces of food: Amici et al., 2008; reversed contingency task using 1:4 pieces: Amici et al., unpublished data). Some studies on numerical abilities in primates have reported a relatively low level of discrimination between food quantities by some primates (e.g., Schmitt & Fischer, 2011). However, these studies included comparisons of pairs like 4:5 or 5:6, which are harder to discriminate than 1:3 because (i) they involve larger numbers (which might require more complex cognitive skills to be processed: see Feigenson et al., 2004), and (ii) they involve pairs of numbers whose ratio is larger and, thus, harder to discriminate (e.g., Hauser et al., 2003). In fact, when the ratio was 1:7 or 2:8 in the familiarization phase, Schmitt & Fischer (2011) found that individuals chose the larger quantity in at least 80% of the trials within no more than two sessions.

The task consisted of one baseline condition, equal and unequal experimental conditions (Table 2). In all conditions, the experimenter gave food

Table 2.
For each condition, quantities of food provided to each subject and number of sessions and trials administered to each dyad.

Condition	Quantity of food	Number of sessions per dyad
Baseline	1-1, 1-1, 1-1, 1-1	1 before and 1 after each equal or unequal condition (= 4 + 4 trials)
Equal	1-3, 3-1, 1-3, 3-1, 1-3, 3-1, 1-3, 3-1	1 (= 8 trials)
Unequal	1-3, 1-3, 1-3, 1-3, 1-3, 1-3, 1-3, 1-3	1 (= 8 trials)
	1-3, 1-3, 1-3, 1-3, 3-1, 3-1, 3-1, 3-1	1 (= 8 trials)

On three different days, each dyad received one session consisting of one experimental condition (i.e., equal or unequal condition), preceded and followed by a baseline condition, randomly selecting the dyads that received the equal or unequal conditions first. Each dyad only underwent each of the three experimental conditions once (i.e., subjects receiving 1 or 3 in the first experimental trial were randomly selected within each dyad and counterbalanced within each species).

to one subject by stretching out her arm in the direction of the subject. The experimenter waited approximately 1 s after food was accepted before providing food to the other subject and interrupted the session (consisting of one experimental condition and two baseline conditions, see below) if more than 120 s elapsed without the subject accepting the food. For all conditions, the positions of the two subjects were randomly assigned.

In the baseline condition, the experimenter gave 1 piece of food to one subject and then 1 piece of food to the other subject, four times in a row (1-1, 1-1, 1-1, 1-1). In the equal condition, the experimenter gave 1 piece of food to the first subject, then 3 pieces of food to the second subject, and in the following trial 3 pieces of food to the first subject, and 1 piece of food to the second subject, four times in a row (1-3, 3-1; 1-3, 3-1; 1-3, 3-1; 1-3, 3-1). In this condition, food was therefore equal in quantity in each of two trials and across the eight trials, although unequally distributed in each trial. This condition allowed us to test subjects' behaviour with an overall equal food distribution, while clearly distinguishing it from the baseline condition. Please note that perceiving this condition as equal might require the ability to extrapolate over (short) time, which has already been documented in some species (capuchin monkeys: Brosnan et al., 2006; orangutans: Dufour et al., 2009). The unequal condition was administered in two different ways. Individuals received different amounts of food, with food either being unequally distributed throughout the eight trials (1-3, 1-3, 1-3, 1-3, 1-3, 1-3, 1-3, 1-3) or being unequally distributed in one direction throughout the first four trials of the session (1-3, 1-3, 1-3, 1-3) and in the other direction in the following four trials of the same session (3-1, 3-1, 3-1, 3-1). Each dyad only underwent each of the unequal conditions once, so that subjects receiving 1 or 3 in the first unequal trial were randomly selected within each dyad and counterbalanced within each species (see Table 2). In the unequal condition, data in which dominants received more food than subordinates were separately analysed from data in which they received less.

Dominants' and subordinates' behaviour was separately analysed, as their expectations about food distribution are predicted to differ (see Chalmeau & Gallo, 1996; de Waal, 1996, 2006; Chalmeau et al., 1997; Werdenich & Huber, 2002; Braeuer et al., 2006, 2009). Each subject was paired with all possible conspecifics. On three different days, each dyad received one session, consisting of one experimental condition, preceded and followed by a baseline condition, randomly selecting the dyads that received the same amount of food or different amounts of food in the experimental condition. If one of the daily sessions was interrupted, the session was *not* repeated on a following day, to (i) ensure that all dyads had the same exposure to the set-up and (ii) avoid biasing the results by disregarding all sessions in which one of the individuals within the dyads refused to accept food. However, each completed condition within interrupted sessions was analysed.

2.3. Data collection and analyses

We videotaped all trials, with the exception of 4 out of 440 trials for the tolerance task, due to technical reasons, and 48 out of 549 sessions for the distribution task, in which the subjects were never visible as they never approached to take the first piece of food within the time limit. Trials were scored on a check-sheet that was later checked against the videotapes for accuracy. A second coder scored 20% of the videotaped sessions for inter-coder reliability, which was high (Spearman's correlation for duration data: $\rho = 0.90$).

In the tolerance task, for each of the two subjects the experimenter coded (i) the time each subject spent drinking alone and (ii) the time each subject spent drinking simultaneously with the partner. Since there were no significant differences in these two measures between the close and far conditions, we combined the scores of the two conditions.

In the food distribution task, for each of the two subjects the experimenter coded (i) the time in the session spent not in proximity to the food source (i.e., being more than 0.50 m from it; proximity avoidance or PA), (ii) the time spent begging the experimenter for food (i.e., subjects stretched out their hand or fingers or presented their lips through the bars), (iii) the time spent banging against the mesh between subjects or between the subject and the tester (BA), (iv) the time spent self-scratching (SS) and (v) the time spent performing aggressive behaviour (i.e., aggressive displays and lunges toward the other subject or the experimenter, AB). For statistical analyses, we used the proportion of PA, time spent begging, BA, SS and AB out of the total time of each session. PA was used as a measure of the subjects' aversion, in that it was considered as a refusal to come close to the food and accept it, thus avoiding continuing participating in the test (e.g., Braeuer et al., 2009; Brosnan et al., 2010). Given that the proportions of time spent banging, performing self-scratching and aggressive behaviours were correlated with one another across individuals ($p < 0.001$, in all cases), we summed them together in a composite measure (BA–SS–AB). Different individuals might show different proportions of these behaviours, but banging, self-scratching and aggressive behaviour should not occur more frequently if subjects perceive the situation as satisfying their expectations about how food should be distributed. Finally, conditions were categorized according to the amount of food received by the dominant subject relative to the subordinate subject in the experimental conditions (i.e., more, less or equal).

We used linear mixed models (LMM) to assess the effect of species on the proportion of time each subject spent simultaneously drinking with the partner out of the total time spent drinking (alone or simultaneously), while controlling for the two subjects' sex combination (e.g., female–female, female–male) and age combination (e.g., adult–adult, adult–juvenile). In the food distribution task, the distribution of interrupted conditions was too uniform to allow reliable statistical analyses. Consequently, we only report descriptive statistics. We used LMM to assess the effects of species, partner's BA–SS–AB and begging on either the subordinate's or dominant's PA. We controlled for the subject's PA in the baseline condition (to control for inter-individual differences in the baseline tendency to avoid proximity to food) and for the two subjects' age combination and sex combination. In all cases, both subjects' identities were included as random factors to control for between-subject variation and non-independence of data points. In the food distribution task, separate models were run for each of the three relative amounts of food received by subjects (the dominant received more, less or as much food as the subordinate). In all cases, we selected the best model using Akaike's information criteria (AIC), which compares the adequacy of several models and identifies the model that best explains the variance of the dependent variable as the model with the lowest AIC value (Burnham & Anderson, 2004; Tabachnick & Fidell, 2007). Only the effects of the independent variables present in the best models are presented. An alpha level of 0.05 was adopted for all tests, but if species was a significant predictor of the dependent variable in the best model, we used pairwise comparisons with Bonferroni adjustments to detect inter-specific differences. All analyses were conducted in SPSS version 17.0.

3. Results

3.1. Tolerance task

The proportion of time subjects spent simultaneously drinking was influenced by species (Table 3; Figure 1). In particular, chimpanzees spent a higher proportion of time simultaneously drinking than gorillas (df = 51, $p = 0.008$), spider monkeys (df = 39, $p = 0.043$), capuchin monkeys (df = 40, $p < 0.001$) and macaques (df = 43, $p < 0.001$). Bonobos spent a higher proportion of time simultaneously drinking than gorillas (df = 48, $p = 0.027$), capuchin monkeys (df = 38, $p < 0.001$) and macaques (df = 41, $p < 0.001$). Orangutans spent a higher proportion of time simultaneously drinking than capuchin monkeys (df = 39, $p = 0.007$) and macaques (df = 41, $p = 0.002$).

Table 3.
Summary of the results of the best LMM to assess social tolerance.

Dependent variable	Independent variable	*F*	df	*p*
Proportion of time spent simultaneously drinking	Intercept	144.921	1, 49	<0.001
	Species	12.300	6, 42	<0.001
	Sex combination	5.020	2, 82	0.009

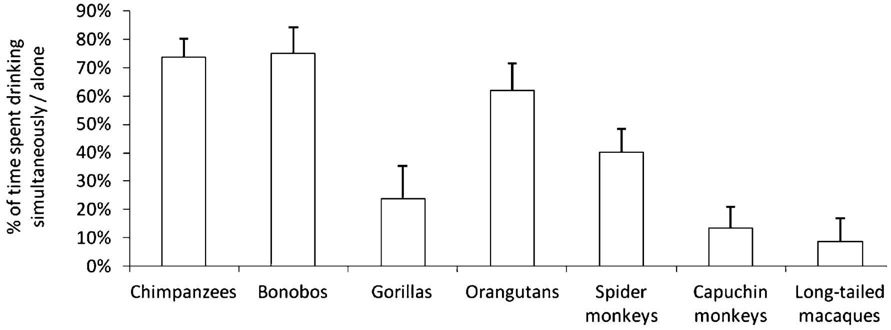

Figure 1. For each species, estimated marginal mean (+ SE) percentage of time in the trial spent simultaneously drinking out of the time spent drinking (alone or simultaneously).

3.2. Food distribution task

Macaques refused to participate in all but 5 sessions by avoiding proximity to food in the first baseline condition of each session, and they were therefore excluded from further analyses (Table 4). Even these 5 sessions were interrupted because of proximity avoidance when one of the experimental conditions was administered. The following analyses on PA are based on only completed conditions.

3.2.1. Dominants received more food than their partners

Dominant bonobos refused to participate in at least one-third of the sessions (Table 4). The proportion of time subordinates avoided proximity to food was positively associated with the proportion of time dominants showed BA–SS–AB, but not with species (Table 5; Figure 2). No effect of any tested variable was detected on the proportion of time dominants avoided proximity (Table 5; Figure 2).

3.2.2. Dominants received as much food as their partners

Dominant bonobos and subordinate capuchin monkeys refused to participate in at least one-third of the conditions (Table 4). No effect of any tested variable was detected on the proportion of time subordinates avoided proximity (Table 6; Figure 3). The proportion of time dominants avoided proximity was instead influenced by species (Table 6). In particular, dominant capuchin monkeys' PA was significantly higher than that of all other species (chimpanzees: df = 26, $p = 0.002$, bonobos: df = 28, $p = 0.023$, orangutans: df = 26, $p = 0.003$, gorillas: df = 24, $p = 0.002$, spider monkeys: df = 22, $p = 0.027$; Figure 3).

Table 4.
For each species and condition, number and percentage of trials in which food was refused by dominants and subordinates, with subsequent interruption of the condition.

Species	Baseline		Dominants received more		Dominants received as much as		Dominants received less		Total interrupted sessions	
	Dom	Sub	Dom	Sub	Dom	Sub	Dom	Sub	Dom	Sub
Chimpanzees	0/81 0%	0/81 0%	0/27 0%	0/27 0%	0/27 0%	0/27 0%	0/27 0%	0/27 0%	0/81 0%	0/81 0%
Bonobos	4/30 13%	0/30 0%	3/9 33%	0/9 0%	3/9 33%	0/9 0%	2/8 25%	0/8 0%	12/30 40%	0/30 0%
Orangutans	0/30 0%	0/30 0%	0/10 0%	0/10 0%	0/10 0%	0/10 0%	0/10 0%	0/10 0%	0/30 0%	0/30 0%
Gorillas	0/30 0%	0/30 0%	0/10 0%	0/10 0%	0/10 0%	0/10 0%	0/10 0%	0/10 0%	0/30 0%	0/30 0%
Spider monkeys	13/63 21%	0/63 0%	0/17 0%	1/17 6%	0/17 0%	0/17 0%	0/16 0%	1/16 6%	13/63 21%	2/63 3%
Capuchin monkeys	6/63 10%	38/63 60%	1/7 14%	0/7 0%	1/6 17%	2/6 33%	1/6 17%	0/6 0%	9/63 14%	40/63 63%
Long-tailed macaques	15/63 24%	43/63 68%	1/3	2/3	–	–	0/2	2/2	16/63 25%	47/63 75%

Dom, dominants; Sub, subordinates. Percentages are only reported when more than 5 trials were administered.

Table 5.
Summary of the results of the best LMM when dominants received more food than their partners.

Dependent variable	Independent variable	*F*	df	*p*
Subordinate's PA	Intercept	3.973	1, 28	0.056
	Dominant BA–SS–AB	73.451	1, 24	<0.001
	Subordinate PA in baseline	6.010	1, 59	0.017
Dominant's PA	Intercept	5.179	1, 68	0.026
	Sex combination	5.314	2, 68	0.007
	Dominant PA in baseline	91.538	1, 68	<0.001

PA, proximity avoidance; BA–SS–AB, banging, self-behaviours and aggressive behaviours.

3.2.3. Dominants received less than their partners

No species refused to participate in more than one-fourth of the conditions. No effect of any tested variable was detected on the proportion of time

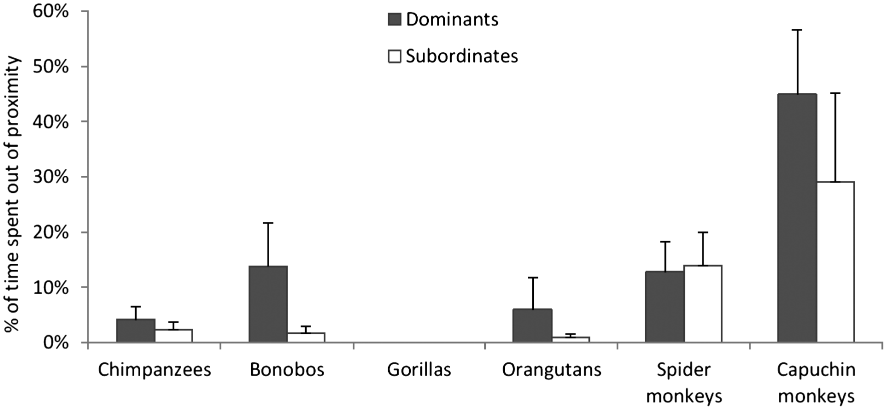

Figure 2. For each species, mean percentage of time in the trial (+ SE) in which dominants (in grey) and subordinates (in white) avoided proximity to food when dominants got more food than subordinates.

Table 6.
Summary of the results of the best LMM when dominants received as much food as their partners.

Dependent variable	Independent variable	*F*	df	*p*
Subordinates' PA	Intercept	0.481	1, 73	0.490
	Subordinate PA in baseline	88.872	1, 73	<0.001
Dominants' PA	Intercept	12.434	1, 37	0.001
	Species	5.085	5, 21	0.003
	Dominant PA in baseline	16.788	1, 69	<0.001

PA, proximity avoidance.

subordinates avoided proximity (Table 7; Figure 4). The proportion of time dominants avoided proximity was instead influenced by species (Table 7). In particular, dominant capuchin monkeys' PA was significantly higher than that of chimpanzees (df $= 33$, $p = 0.002$), orangutans (df $= 28$, $p = 0.014$), gorillas (df $= 25$, $p = 0.004$) and spider monkeys (df $= 27$, $p = 0.002$; Figure 4).

4. Discussion

Our test on social tolerance provided the first direct comparison of the degree of strictness in dominance relationships across the seven study species.

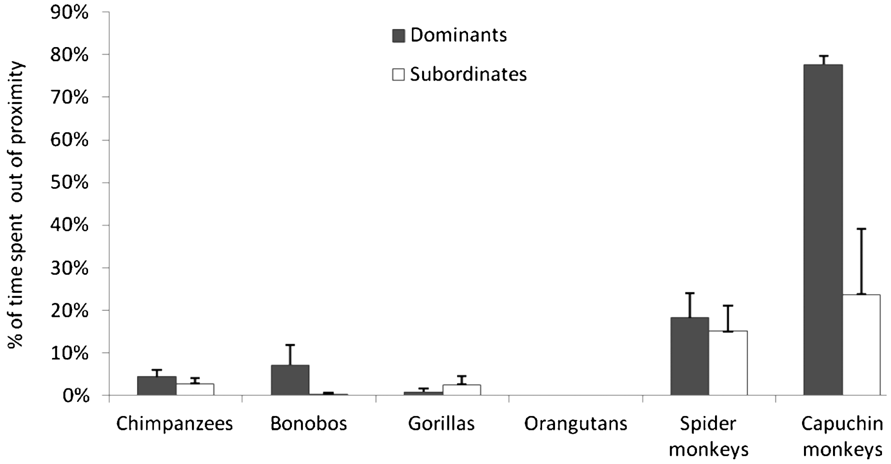

Figure 3. For each species, mean percentage of time in the trial (+ SE) in which dominants (in grey) and subordinates (in white) avoided proximity to food when dominants got as much food as subordinates.

Table 7.
Summary of the results of the best LMM when dominants received less food than their partners.

Dependent variable	Independent variable	*F*	df	*p*
Subordinates’ PA	Intercept	3.047	1, 25	0.093
	Subordinate PA in baseline	14.545	1, 74	<0.001
Dominants’ PA	Intercept	10.768	1, 31	0.003
	Species	4.641	5, 16	0.008
	Dominant PA in baseline	16.496	1, 70	<0.001

PA, proximity avoidance.

The more tolerant species were chimpanzees and bonobos, followed by orangutans, spider monkeys, gorillas, brown capuchin monkeys and long-tailed macaques (Figure 1). Overall our results confirm what already evidenced in other studies analysing social tolerance in one or few species. In particular, chimpanzees and bonobos are reported to be relatively tolerant species, although bonobos are generally considered less competitive and more tolerant than chimpanzees (de Waal, 1989; Hare et al., 2007; but see Jaeggi et al., 2010). Orangutans are also considered to be moderately tolerant (van Schaik, 2003; Singleton et al., 2009). Similarly, spider monkeys are re-

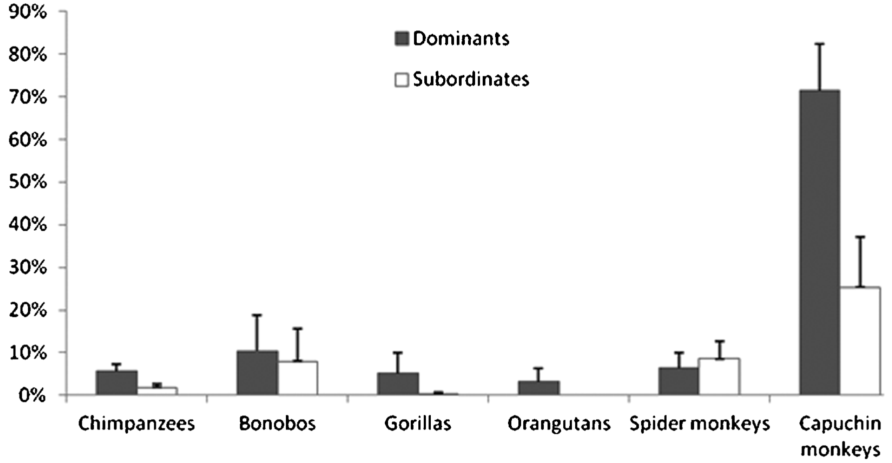

Figure 4. For each species, mean percentage of time in the trial (+ SE) in which dominants (in grey) and subordinates (in white) avoided proximity when dominants got less food than subordinates.

ported to be relatively tolerant among monkey species (Aureli & Schaffner, 2008). On the contrary, gorillas are characterized by social avoidance and intolerance of others (Byrne, 1999; Stoinski et al., 2003; Lonsdorf et al., 2009), and long-tailed macaques are considered a rather despotic species (Thierry, 2007). The only contrasting finding was related to brown capuchin monkeys, which are usually reported to be relatively tolerant (e.g., de Waal, 1997), although in our test they showed an unexpected low level of tolerance. Interestingly, the degree of strictness of dominance relationships appears to reflect the degree of fission–fusion dynamics and inhibition that has already been evidenced across the same species (Amici et al., 2008).

In the food distribution task, dominant and subordinate chimpanzees, orangutans and gorillas participated in all the sessions. These results fit the reported chimpanzees' pattern with typically high participation levels in similar experimental tasks (e.g., Braeuer et al., 2009). On the contrary, bonobos and spider monkeys refused participating in some sessions across all conditions. However, caution is needed while interpreting bonobos' data because the most dominant female was responsible for all refusals, in contrast to what happened in the other species, in which more subjects refused to participate in the task. The species most refusing to participate were capuchin monkeys and especially long-tailed macaques, which refused taking part in most conditions. Overall, the patterns of refusal of participation seem to reflect the inter-specific differences in social tolerance, with less tolerant species participating less in the food distribution task. Refusals of participation seem not to be homogeneously distributed between dominants and subordinates across different species. Whereas dominant subjects were responsible for most refusals of participation in bonobos and spider monkeys, subordinate subjects were responsible for most refusals in capuchin monkeys and long-tailed macaques (see Table 4). One might speculate that subordinates in less tolerant species show more aversion to unexpected food distributions, as is the case in capuchin monkeys and long-tailed macaques, out of fear of retaliation from the dominants (but see Massen et al., 2012 for subordinate long-tailed macaques not showing aversion when receiving MVF). In contrast, subordinates in more tolerant species would not fear unexpected food distributions, and dominants may, thus, show relatively more aversion to the unexpected food distributions, as is the case in spider monkeys and bonobos.

In the food distribution task, no effect of species was detected on dominant and subordinate subjects' proximity avoidance when dominants received more food than their partners. Dominants receiving more food is possibly an expectation common to all species and, thus, elicits similar responses across all tested species (although dominant capuchin monkeys seemed to avoid proximity more than other species; Figure 2). Interestingly, when dominants received more food than their partners, subordinates avoided proximity to food for longer when dominants displayed more BA–SS–AB. Although LMM cannot detect the direction of causality, it seems plausible that subordinates monitor their dominant partners during the trial, and limit potentially conflicting situations with them by avoiding proximity to the food source more often when the dominant partner shows higher levels of aggression, self-directed behaviours or banging. It is unclear, however, why this effect was evidenced only in this condition.

Species differences in aversion when dominants received as much as or less than subordinates confirm de Waal's (2006) hypothesis that species differ in the responses to different food distributions accordingly to their expectations. For example, dominant capuchin monkeys avoided proximity to the food more than the other species. Thus, at least when no effort is required, capuchin monkeys did not expect food to be equitably distributed and showed aversion when this happened. As Brosnan (2006) suggested, dominants are accustomed to usually receiving more food than subordinates (instead of as much food as or less than them) even in relatively tolerant species.

Our findings show that long-tailed macaques were the most extreme in their responses, refusing to participate in the task when the baseline condition was first administered in all but five sessions. Possibly, although we conceived this condition as a baseline, macaques perceived it as an equal distribution of food between dominants and subordinates. Their extremely high refuse to participate might, therefore, reflect macaques' aversion toward all food distributions that do not favour dominants since they probably expect subordinates to receive nothing at all. This view matches both long-tailed macaques' relative high degree of intolerance that we found in the tolerance task and their despotic nature reported in observational studies (Thierry, 2007). Our findings however are in contrast with those of Massen et al. (2012), who found that long-tailed macaques rarely show aversion when receiving food with no effort.

In our study, brown capuchin monkeys unexpectedly behaved more similarly to long-tailed macaques than any other species we tested, showing little tolerance in the tolerance task and avoiding proximity to food whenever food distributions did not favour dominants. Note that capuchin monkeys and long-tailed macaques' avoidance in these tasks cannot be attributed to lack of motivation or uneasiness to the experimenter and the set-up, as all the subjects have also been individually tested in a series of other cognitive tasks in which they kept proximity and participated in the tasks administered by the same experimenter, with very similar set-ups (see Amici et al., 2008, 2009a,b, 2010). Similarly to our results, some field studies seem to question the degree of social tolerance in brown capuchin monkeys, as food competition can be high and social tolerance seems to be limited to specific dyads, with dominants usually being highly despotic in feeding contexts (Janson, 1985, 1996; Tiddi et al., 2011). Recently, other experiments have confirmed a low level of social tolerance in the same group of captive capuchin monkeys (Burkart & Kosonen, pers. commun.). However, experimental studies on other groups provide evidence showing brown capuchin monkeys as a tolerant and relatively cooperative species (e.g., de Waal, 1997; Brosnan & de Waal, 2003). This contrast suggests that there might be a large variation in the degree of social tolerance and expectations of food distributions between partners across different groups of brown capuchin monkeys. Whether this variation transcends methodological differences and is instead due to developmental factors related to group dynamics and living conditions is a matter deserving further study. For example, although similar visual and physical contact was guaranteed for all the dyads we tested, future tasks should ideally avoid situations in which some dyads are separated from each other during testing whereas other dyads are not. Moreover, a larger sample of subjects would also allow controlling for intra-specific differences in social tolerance. This would be especially important if considering that social tolerance levels do not only vary across species, but also within species, with possible consequences also in terms of cognition (e.g., Melis et al., 2006; Hare et al., 2007; Braeuer et al., 2009). Interestingly, like in Braeuer et al. (2006, 2009), the four great apes did not differ in their responses in any of the conditions of the food distribution task, although the most dominant bonobo female appeared to refuse participation more than any other great ape.

In conclusion, individuals' proximity avoidance varied across species and this variation appeared to at least partially reflect the inter-specific differences in the strictness of dominance relationships as measured in the tolerance task, with less tolerant species (i.e., brown capuchin monkeys and long-tailed macaques) responding more negatively to food distributions not favouring dominants as if their expectations about how food is usually consumed among group members were violated. Although we found no inter-specific differences in the food distribution task among the other species, it is conceivable that other more refined tasks may detect those differences. This, however, remains to be elucidated by future studies using simple paradigms that allow direct comparisons across further species while considering the often underestimated aspect that subjects may have different expectations about how food should be distributed depending on the species they belong and their dominance rank relative to the partners.

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