

Variation in withholding of information in three monkey species

Federica Amici^{1,2,3,4,*}, Josep Call² and Filippo Aureli¹

¹*Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF, UK*

²*Department of Comparative and Developmental Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*

³*Unit of Cognitive Primatology and Primate Center, Institute of Cognitive Sciences and Technologies, CNR, Rome, Italy*

⁴*Research Group Behavioural Biology, Ethologie Station, Utrecht, The Netherlands*

Studies on tactical deception have reported that informed subordinates can withhold information from naive dominants, but they have not directly compared species' performance. Here, we compared the performance in two withholding-of-information tasks of three monkey species differing in the strictness of their dominance hierarchy and degree of fission–fusion dynamics: spider monkeys, capuchin monkeys and long-tailed macaques. Food was hidden from the dominants' view either inside an opaque box or in a transparent box that could only be opened by knowledgeable subordinates. All species were capable of withholding information, with subjects refraining from interacting with the box when the dominant was nearby. Spider monkeys were the most efficient at retrieving food, by timing it when the dominant was far from the box. Capuchin monkeys were also quite efficient when alone at the box, but they lost much of the food when manipulating the box with the dominant nearby. The results supported our predictions based on interspecific differences in the strictness of the dominance hierarchy and the degree of fission–fusion dynamics, with the former constraining the subjects' tendency to approach the box and the latter affecting the subjects' tendency to wait for the appropriate situation to retrieve the food.

Keywords: tactical deception; comparative cognition; inhibition; spider monkeys; capuchin monkeys; long-tailed macaques

1. INTRODUCTION

Byrne & Whiten (1985) proposed to use the general term 'tactical deception' to include all the 'acts from the normal repertoire of an individual, used at low frequency and in contexts different from those in which it uses the high frequency (honest) version of the act, such that another familiar individual is likely to misinterpret what the acts signify, to the advantage of the actor' (p. 672). Under this broad functional definition, tactical deception can be based on various sorts of social representations ranging from the detection of specific cues (e.g. face) to the inference of more abstract mental states (e.g. seeing). Regardless of the precise social representation involved, tactical deception seems to rely on efficient learning abilities, sensitivity to a wide range of subtle social cues and flexibility in using them (Cheney & Seyfarth 1990; Byrne & Corp 2004). Consequently, the term 'tactical deception' can be used to refer not only to representing others' mental states (i.e. mindreading or theory of mind) but also to the inhibition of behaviours in the appropriate circumstances (e.g. when negative responses by others are expected).

The first reports of tactical deception came mostly from anecdotal observations of free-ranging primates

(see Whiten & Byrne 1988 for a review). Experimental studies on several primate species attempted to replicate these findings in more controlled settings, mainly with subjects learning to deceive an experimenter as to the location of a hidden reward by pointing to empty food containers in the presence of 'competitive' human trainers (Woodruff & Premack 1979; Povinelli *et al.* 1990; Kummer *et al.* 1996; Mitchell & Anderson 1997; Anderson *et al.* 2001). However, the training required with this procedure suggested that the deceptive behaviour was nothing more than simple conditional discrimination learning.

The 'informed forager' paradigm was proposed as a better experimental approach for the study of tactical deception because it more closely resembles natural conditions by using competitive situations to investigate social tactics, not requiring training procedures and only involving conspecifics (Hare 2001; Fujita *et al.* 2002). In Menzel's (1974) classic study, a subordinate chimpanzee was previously informed about the position of a favourite food and then allowed to search for it in the presence of a dominant partner. The subordinate learned to avoid retrieving the food in the dominant's presence and even learned to lead the dominant away from the food (see also Hirata & Matsuzawa 2001). The occurrence of such withholding-of-information behaviour was also demonstrated in Old World monkeys (Coussi-Korbel 1994; Ducoing & Thierry 2003), but contrasting results were found for capuchin monkeys and lemurs

*Author for correspondence (abbepu@yahoo.it).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0759> or via <http://rspb.royalsocietypublishing.org>.

(Deaner 2000; Fujita *et al.* 2002; Hare *et al.* 2003; Genty & Roeder 2006; Genty *et al.* 2007).

Although withholding of information has also been documented in a few species other than non-human primates (including ravens and human infants from a very young age: Bugnyar & Kotrschal 2004; Bugnyar & Heinrich 2005; Reddy 2007), no systematic comparison following exactly the same paradigm has ever been conducted across species. To fill this gap, we followed Menzel's (1974) withholding-of-information procedure and tested spider monkeys (*Ateles geoffroyi*), brown capuchin monkeys (*Cebus apella*) and long-tailed macaques (*Macaca fascicularis*). All these species live in complex social systems, but differ in their phylogenetic relatedness and social structure (Fragaszy *et al.* 2004; Thierry 2007; Aureli & Schaffner 2008). We predicted that, being advantageous in complex social systems by allowing individuals to better offset the costs of high competition (Whiten & Byrne 1988), tactical deception in the form of behavioural inhibition and withholding of information would be found in all three monkey species, with knowledgeable subordinates refraining from retrieving food in the presence of dominants. We also predicted that the frequency of such tactical deception might vary across species as a function of their social structure. In particular, in species with a strict dominance hierarchy, such as long-tailed macaques (Thierry 2007), subordinates might be so intimidated by the presence of dominants to completely refrain from retrieving food in most cases. In these species, social interactions are indeed strictly conditioned by dominance relationships with the access to resources being monopolized by higher ranking individuals and the usurping of dominance privileges often being punished by retaliation from dominants (Thierry 2007). In contrast, in species with a more relaxed dominance hierarchy, such as capuchin monkeys (de Waal 1997), individuals show more tolerance when interacting with other group members, so that subordinates are expected to take a small risk by trying to retrieve food in the presence of dominants and thus act more flexibly than long-tailed macaques. Spider monkeys also have a more relaxed dominance hierarchy than long-tailed macaques and experience a higher degree of fission–fusion dynamics (i.e. frequent changes in subgroup size and composition) than the two other species (Aureli & Schaffner 2008). The latter characteristic is possibly associated with enhanced inhibitory skills and behavioural flexibility (Amici *et al.* 2008; Aureli *et al.* 2008). Consequently, we expected spider monkeys to be the most efficient species at retrieving food in the presence of dominants by withholding information when the dominant was close to the food location, but by promptly retrieving the food after the dominant left.

2. METHODS

(a) Subjects

We tested 9 spider monkeys at the Centenario Zoo in Merida, Mexico, 7 brown capuchin monkeys at the ISTC-CNR Primate Center in Rome, Italy, and 10 long-tailed macaques at the Research Group Behavioural Biology, University of Utrecht, The Netherlands. Subjects were all housed in social groups and were of both sexes and of various ages and dominance ranks (previously determined according

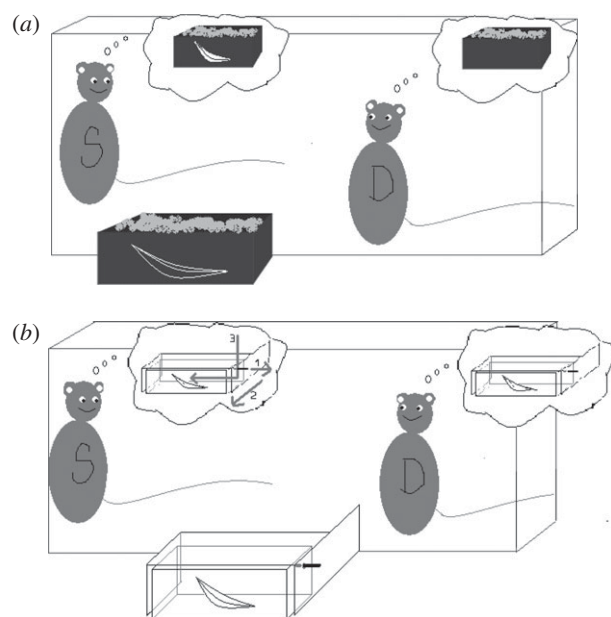


Figure 1. Experimental set-up for the two tasks. (a) In OB, the subordinate subject (S) is informed about the presence of a preferred food item hidden inside an opaque box, while the dominant partner (D) is not informed. (b) In CB, the preferred food item is visible to both S and D, but only S is informed about the way to access it, by first taking the peg off, secondly pushing the box open and finally retrieving the food.

to differential access to juice and food resources in pair tests; see electronic supplementary material, table S1). All subjects were accustomed to being temporarily isolated in testing rooms and were tested by the same familiar experimenter. Prior to this study, all subjects had received a series of cognitive tasks (e.g. Amici *et al.* 2008) but none of the subjects had been previously tested in a social-inhibition/withholding-of-information task. Subjects were never deprived of food or water at any time before or during the experiment.

(b) Materials and procedure

During the tasks, each subject was tested together with a dominant partner by isolating them in the testing room (figure 1). A contiguous room allowed us to temporarily isolate the dominant partner during the beginning of each session, so that the subject in the testing room could not be seen by the dominant partner. Both the testing room and the contiguous room could not be seen by the rest of the group, so as not to compromise the other subjects' naivety. All testing rooms were sufficiently large (capuchin monkeys: $2 \times 2.3 \times 2.8$ m; macaques: $3 \times 3 \times 2$ m; spider monkeys: triangular base with edges approx. 2.1, 2.1 and 3 m, and 3 m height) to allow the subordinate to access and eat the food before the dominant could approach and steal the food. A box (approx. $30 \times 50 \times 20$ cm) was placed in front of the testing room so that both the subject and the dominant partner could reach for its content through the mesh. Depending on the task, the box could be either opaque and filled with scrap paper (in the opaque box task, hereafter OB) or transparent (in the clear box task, hereafter CB). In OB, food could be simply hidden below the scrap paper. In CB, food was visible but could only be accessed by taking a little peg off, thus allowing the lateral transparent lids to slide in the direction opposite to the subject. In this way,

the food could be accessed through one of the two opened lateral sides (see electronic supplementary material S2).

In OB, we tested whether subjects could withhold information about the presence of food inside the box. In the solitary condition, only the subject was in the testing room. In full view of the subject, the experimenter hid pieces of banana or little balls of agglomerated raisins in the box and then pushed the box closer to the testing room within the subject's reach. In the no-barrier experimental condition the procedure was identical but, shortly before pushing the box closer to the testing room and just after having baited it, the dominant was allowed to enter the room. Having been in the contiguous room, the dominant had not seen the box being baited. In the barrier experimental condition, the procedure was identical to the previous one, but an opaque partition (approx. 50 × 60 cm) was placed inside the testing room so that the box could be accessed by both individuals from either side of the partition, allowing subjects to retrieve the food by moving on the side of the barrier opposite to where the dominant partner was.

In CB, we tested whether subjects could withhold information about how to open the box containing visible food. We increased the dominant's tendency to approach the box by making the food visible to both her and the subject, thus increasing the situations in which the subordinate had to be especially wary of approaching the box and retrieving the food. Prior to the testing phase, subjects and dominant partners received training with the box. First, each individual was trained to open the box when the peg was already off, by simply pushing the lateral lids forward and accessing the food from one side. Second, only the subordinate of each possible dyad was trained to open the box when the peg was still on. Upon efficiently completing the training (i.e. when food was efficiently retrieved in five consecutive trials), subjects received two conditions. The solitary condition was identical to the solitary OB condition, whereas the experimental condition was identical to the no-barrier OB condition. In both conditions, the subject could obtain the food by taking the peg off, pushing the lateral lids forward and retrieving the food. In the experimental condition, however, once the peg was removed by the subject, the dominant could also retrieve the food by pushing the lateral lids forward.

In both tasks, each session was concluded after the food had been retrieved or after 5 min from its beginning. The dominant underwent the control conditions only after having terminated her role as the naive partner. In OB, each subject was tested with only one among all the possible dominant partners, receiving two trials for the solitary condition and two for each experimental condition in each of two consecutive days. Given the sample size limit imposed by the number of individuals in each social group and to improve the power of our analysis, in CB we increased the number of dyads by testing each subject with all possible dominant partners. It is likely that the difficulty in opening the box, combined with the subject's speed in doing so, prevented dominants from acquiring the skills necessary to open the box simply by observing subordinates. In fact, no dominant partner opened the box by herself during the testing phase. This difficulty was confirmed by the high number of trials necessary to train subjects to open the box when the peg was still on prior to the testing phase. On different days, each subject received two trials for the solitary condition, two daily trials with each dominant partner for three consecutive days, and two more trials for the solitary

condition. CB conditions were only run after all OB conditions were over, to avoid compromising the dominants' naivety about the presence of food inside the box.

(c) Scoring and data analysis

All trials were videotaped and later scored from the videotapes. A second observer coded 25 per cent of all the trials to assess the interobserver reliability of the subjects' behaviours. Interobserver reliability was high (Cohen's $k = 0.95$).

In the solitary conditions, the experimenter coded the subject's behaviours indicating motivation to retrieve food with no potential social interference: (i) time for the subject to retrieve food; (ii) percentage of time in the trial spent in proximity to the box (i.e. being within 50 cm of the box). In the experimental conditions, the experimenter additionally coded time spent (iii) by the dominant and (iv) by the two individuals together in proximity to the box; whether the subject (v) only approached the box or (vi) retrieved the food when the dominant was not in proximity to the box; (vii) aggressive interactions; and (viii) the individual's position relative to the barrier when the food was retrieved (in OB).

For each subject, we averaged all the behavioural measures across trials of the same condition. In OB, subjects never retrieved the food when the dominant was on the opposite side of the partition (with the exception of one capuchin monkey), and there were no significant differences in any measure between the no-barrier and barrier experimental conditions. Consequently, in OB we re-ran the statistical analyses at the individual level (each subject), combining all the measures for the no-barrier and barrier experimental conditions and presented only these analyses. As subjects were tested with all possible dominant partners in CB, statistical analyses were run at the dyadic level (by averaging each measure across trials for each dyad).

In case of interspecific differences in the solitary condition (probably due to interspecific differences in motivation), we compared species' behaviours in the experimental condition after dividing each measure for its corresponding behaviour in the solitary condition. The percentage of time the subject spent in proximity to the box together with the dominant was divided by the percentage of time the subject spent in proximity to the box in the solitary condition. In the experimental conditions, we also calculated the percentage of trials in which subjects were 'efficient' at approaching the box and retrieving the food when the dominant was not in proximity to the box. Approaching the box or retrieving the food in the dominant's presence was considered 'inefficient' because each possibly elicited the dominant's interest in the box, allowing the dominant to steal the food from the subordinate. Completely refraining from approaching the box or retrieving the food was also considered inefficient because the subject had no chance to obtain the food.

We used non-parametric statistics to analyse the effect of condition (Wilcoxon test) and species (Kruskal–Wallis test) on the recorded behaviours. When the result of the Kruskal–Wallis test was significant, we used Mann–Whitney tests for pairwise comparisons (Cohen & Cohen 1983). All tests used exact and two-tailed probability, and the α -level was set at 0.05.

3. RESULTS

When comparing the solitary and the experimental OB conditions for each species, spider monkeys spent

significantly less time in proximity to the box in the experimental condition, while macaques retrieved the food significantly later (table 1). Moreover, in CB all species differed in both percentage of time spent in proximity to the box and latency to retrieve the food (table 1). The latency to retrieve the food was significantly longer in the experimental than in the solitary condition. The opposite was true for the percentage of time the subordinate spent in proximity to the box.

In the solitary condition, we found interspecific differences in the latency to retrieve food in CB and in the percentage of time spent in proximity to the box in both tasks (table 2).

When controlling the performance in the experimental OB condition for that in the solitary condition, species significantly differed in the percentage of time subjects spent in proximity to the box together with dominant partners (table 2). In particular, capuchin monkeys spent significantly more time close to the box together with the dominant than spider monkeys ($N_1 = 6$, $N_2 = 8$, $U = 5$, $p = 0.007$). In the experimental condition, there were no interspecific differences in the percentage of efficient trials at approaching the box or retrieving the food (i.e. when the dominant was not in proximity to the box; figure 2a, table 2).

Only in a few experimental OB trials did the dominant approach the box at least once. Statistical analyses could not be run for these trials because the sample size was too small (spider monkeys: 3 trials; capuchin monkeys: 11 trials; macaques: 0 trials). In these trials, spider monkey subjects always approached the box, spent time close to it or retrieved the food when the dominant was distant from the box. Capuchin monkeys approached the box when the dominant was also in proximity to the box in three trials; they spent a mean time of 10 s close to the box together with the dominant; and they retrieved the food while the dominant was also in proximity to the box (four trials), while the dominant was distant from the box (four trials) or they did not retrieve it at all (three trials). In OB, aggression by the dominant towards the subject always occurred after the subject retrieved the food (two trials for spider monkeys, five for capuchin monkeys and one for macaques).

When controlling the performance in the experimental CB condition for that in the solitary condition, species significantly differed in the latency to retrieve the food and in the percentage of time spent in proximity to the box alone and together with the dominant (table 2). Moreover, there were interspecific differences in the percentage of efficient trials at approaching the box and retrieving the food (i.e. when the dominant was not in proximity to the box; figure 2b, table 2). In particular, spider monkeys ($N_1 = 15$, $N_2 = 21$, $U = 64$, $p = 0.002$) and capuchin monkeys ($N_1 = 21$, $N_2 = 21$, $U = 80$, $p < 0.001$) were significantly more efficient than macaques at approaching the box. Spider monkeys were also more efficient than capuchin monkeys ($N_1 = 15$, $N_2 = 21$, $U = 46$, $p < 0.001$) and macaques ($N_1 = 15$, $N_2 = 21$, $U = 55$, $p = 0.001$) at retrieving the food.

The number of experimental trials in which the dominant approached the box at least once in CB was higher than in OB (spider monkeys: 34 trials; capuchin monkeys: 104 trials; macaques: 8 trials), showing that the visible food stimulus was effective in increasing the tendency of

dominants to approach the box and allowing statistical comparisons. In these trials, species significantly differed in the percentage of efficient trials (box approaching: $\chi^2(2) = 18.762$, $p < 0.001$; food retrieval: $\chi^2(2) = 6.753$, $p = 0.034$). In particular, capuchin monkeys were more efficient at approaching the box than spider monkeys ($N_1 = 11$, $N_2 = 21$, $U = 21.5$, $p < 0.001$) and macaques ($N_1 = 3$, $N_2 = 21$, $U = 0$, $p < 0.001$). However, spider monkeys were more efficient at retrieving the food than capuchin monkeys ($N_1 = 11$, $N_2 = 21$, $U = 56$, $p = 0.01$). In CB, aggression by dominants towards subjects occurred in one trial for spider monkeys and three for capuchin monkeys. In these trials, aggression towards subjects occurred after they retrieved the food.

4. DISCUSSION

All species retrieved the food earlier and spent more time in proximity to the box in the solitary than in the experimental CB condition. Results in OB pointed in the same direction, although most of the analyses did not reach statistical significance, probably because of the larger statistical power and motivational incentive in CB. In the experimental CB condition, spider monkeys and capuchin monkeys attempted to get the food (by efficiently approaching the box when the dominant was not in proximity to the box) more often than macaques. Moreover, spider monkeys were more efficient than capuchin monkeys and macaques at retrieving food, by timing it when the dominant was not in proximity to the box. Spider monkeys and macaques tried to get the food mostly when they were alone close to the box, whereas capuchin monkeys showed no clear preference. Finally, spider monkeys were more efficient than capuchin monkeys at getting the food when the partner also approached the box in CB, whereas macaques rarely attempted to get the food under those circumstances.

A study on capuchin monkeys showed their ability to spontaneously monitor the behaviour of dominant partners before retrieving food in a competitive context, but without being sensitive to what the dominant could or could not see (Hare *et al.* 2003). In another study, two of four subordinate capuchin monkeys learned to withhold information, but the study provided no clear indication of spontaneous deception (Fujita *et al.* 2002). Our results support the findings from Hare *et al.* (2003) by showing that all species promptly modified their behaviour in the presence of a dominant partner. Furthermore, such behaviour modification allowed subordinates to outwit a dominant competitor in spider monkeys and capuchin monkeys. Consequently, this study provides evidence for tactical deception in two New World monkeys comparable in some ways to that reported in Old World monkeys and apes (Menzel 1974; Coussi-Korbel 1994; Hirata & Matsuzawa 2001; Ducoing & Thierry 2003).

Although our results provide evidence of inhibition of approaching and retrieving food in the presence of dominant partners, it is unclear whether the subjects also engaged in some form of mindreading, e.g. representing some concept of information that they strived to withhold from dominants. In fact, the lack of use of the barrier suggests that they did not take the dominants' visual

Table 1. For each species and task, mean (\pm s.e.) latency to retrieve food and percentage of time spent in proximity to the box in the solitary and in the experimental conditions. For each species and task, we also show pairwise comparisons of these two behaviours between the solitary and the experimental conditions using Wilcoxon tests. Significant differences are presented in bold. OB, opaque box task; CB, clear box task.

species	task	solitary condition (mean \pm s.e.)		experimental condition (mean \pm s.e.)		solitary versus experimental conditions (Wilcoxon test)	
		latency to retrieve food (s)	% time in proximity	latency to retrieve food (s)	% time in proximity	latency to retrieve food (s)	% time in proximity
spider monkeys	OB	8.7 \pm 3.0	95.3 \pm 4.3	55.7 \pm 35.4	63.5 \pm 13.4	N = 7; T = 31; <i>p</i> = 0.070	N = 6; T = 21; <i>p</i> = 0.031
	CB	31.8 \pm 12.7	89.7 \pm 4.4	75.0 \pm 25.9	69.8 \pm 8.4	N = 11; T = 105.5; <i>p</i> = 0.007	N = 11; T = 74; <i>p</i> = 0.003
capuchin monkeys	OB	4.1 \pm 0.6	86.8 \pm 6.5	57.8 \pm 35.9	71.2 \pm 10.7	N = 5; T = 15; <i>p</i> = 0.063	N = 5; T = 18; <i>p</i> = 0.156
	CB	73.4 \pm 10.3	73.3 \pm 2.9	221.3 \pm 23.7	29.6 \pm 7.0	N = 17; T = 219; <i>p</i> < 0.001	N = 19; T = 222; <i>p</i> < 0.001
long-tailed macaques	OB	70.4 \pm 31.1	36.5 \pm 11.0	174.4 \pm 49.8	23.6 \pm 13.1	N = 7; T = 28; <i>p</i> = 0.016	N = 5; T = 2; <i>p</i> = 0.297
	CB	20.3 \pm 9.6	95.2 \pm 3.3	209.8 \pm 21.0	23.7 \pm 5.9	N = 20; T = 230; <i>p</i> < 0.001	N = 20; T = 210; <i>p</i> < 0.001

Table 2. For each species and task, mean (\pm s.e.) latency to retrieve food and percentage of time spent in proximity to the box in the solitary condition, mean (\pm s.e.) percentage of efficient trials in approaching the box and retrieving the food in the experimental condition, and mean (\pm s.e.) latency to retrieve food, percentage of time spent in proximity to the box alone and together with the dominant in the experimental condition controlled for the same behavioural measures in the solitary condition. For each task, we also show interspecific comparisons of these different behavioural measures using Kruskal–Wallis tests (with Mann–Whitney pairwise comparisons). Significant results are presented in bold. OB, opaque box task; CB, clear box task; S, spider monkeys; C, capuchin monkeys; M, long-tailed macaques.

species	solitary condition		experimental condition		experimental/solitary condition		
	latency to retrieve food (s)	% time in proximity	% efficient at box approaching	% efficient at food retrieving	latency to retrieve food	% time in proximity together	
spider monkeys	OB	8.7 \pm 3.0	95.3 \pm 4.3	87.5 \pm 12.5	87.5 \pm 12.5	15.3 \pm 11.7	0.6 \pm 0.1
	CB	31.8 \pm 12.7	89.7 \pm 4.4	70.0 \pm 6.7	77.8 \pm 8.7	4.7 \pm 2.4	0.7 \pm 0.1
capuchin monkeys	OB	4.1 \pm 0.6	86.8 \pm 6.5	87.5 \pm 8.5	70.8 \pm 16.4	17.4 \pm 11.8	0.8 \pm 0.1
	CB	73.4 \pm 10.3	73.3 \pm 2.9	73.8 \pm 4.4	26.2 \pm 8.0	5.1 \pm 1.1	0.4 \pm 0.1
long-tailed macaques	OB	70.4 \pm 31.1	36.5 \pm 11.0	42.9 \pm 17.0	42.9 \pm 17.0	16.2 \pm 11.5	0.5 \pm 0.2
	CB	20.3 \pm 9.6	95.2 \pm 3.3	34.1 \pm 7.5	34.1 \pm 7.6	49.7 \pm 10.5	0.3 \pm 0.1
Kruskal–Wallis test: χ^2			5.722	4.704	0.297	1.480	11.706
			28.266	16.593	19.151	14.994	23.677
<i>p</i> -values (d.f. = 2)			0.001	0.095	0.862	0.477	0.003
pairwise comparisons			<0.001	<0.001	<0.001	0.001	<0.001
			(–)	(–)	(–)	(–)	C>S
			S=C>M	S>C=M	M>C=S	S>C=M	C>M
			M>S>C	S=C>M	M>C=S	S>C=M	C>M

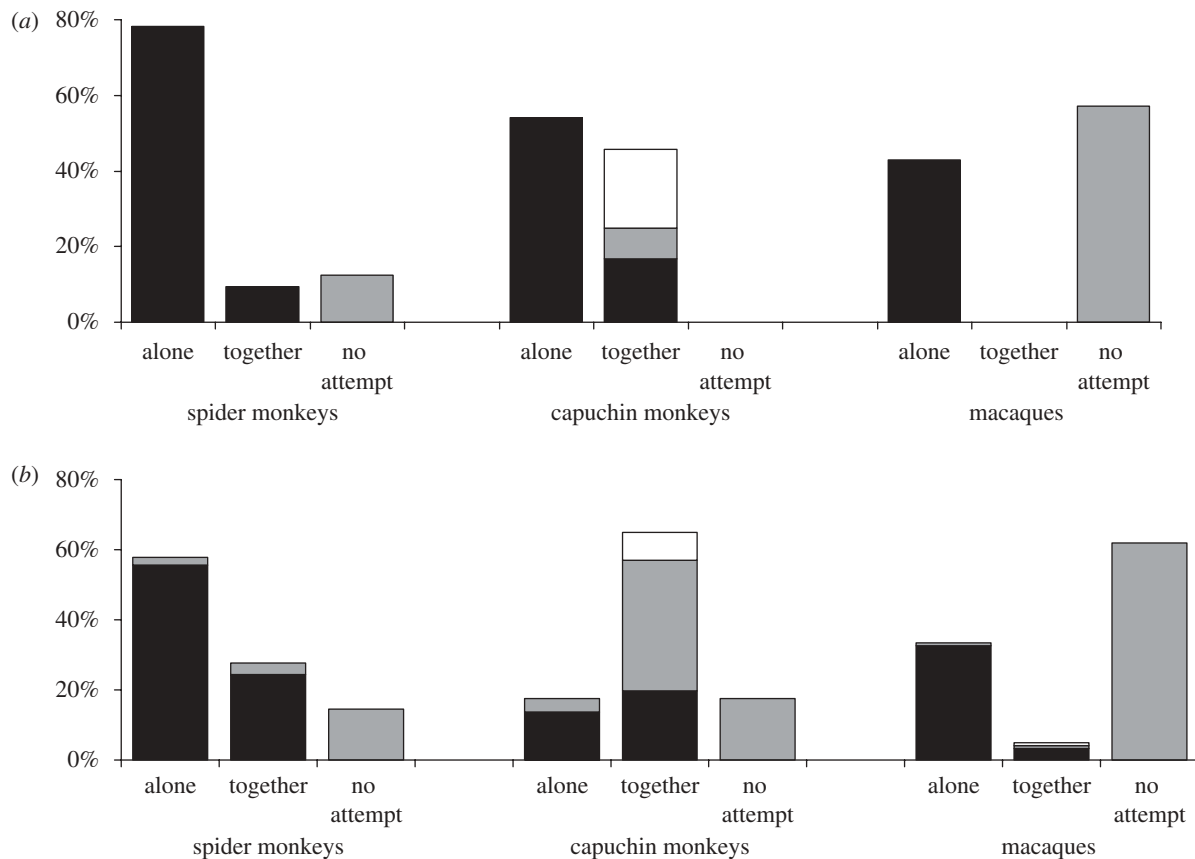


Figure 2. Percentage of trials in which the food was retrieved by the subject, by the dominant or by nobody, as a function of task, species and subjects' strategy (alone: the subject only approached the box without the dominant; together: the subject approached the box together with the dominant; no attempt: the subject never approached the box). (a) Opaque box and (b) clear box. White bar, dominant retrieves food; grey bar, nobody retrieves food; black bar, subject retrieves food.

perspective into account. This means that although the subjects' behaviour served to withhold information from the dominant (who was deceived and did not retrieve the food), it was not based on representing information about the dominant's knowledge. Nevertheless, our results are consistent with the hypothesis that withholding of information of this sort is widespread across species living in complex social systems (Byrne & Whiten 1988; Whiten & Byrne 1988). In contrast to other findings, however, rather than using different *individual* tactics (e.g. avoiding being followed, stopping when being watched or taking a wrong direction; Ducoing & Thierry 2003), our subjects *overall* refrained from interacting with the box when the dominant was present.

The use of the same paradigm with three different species revealed intriguing interspecific similarities and differences. Although all species were capable of withholding information in its broader sense, spider monkeys were the most efficient in retrieving the food in the experimental condition, both when the dominant approached the box and when she did not. Capuchin monkeys were also quite efficient when alone near the box, but they lost much of the food when manipulating the box with the dominant nearby. The possibility that capuchin monkeys were engaging in co-feeding (de Waal 1997) seems to be ruled out by the occurrence of aggression towards the subject after retrieving the food. In contrast, spider monkeys rarely lost the food to the dominant. It is unclear whether this was due to a higher respect for possession in spider monkeys when

compared with capuchin monkeys (cf. Kummer & Cords 1991) or to spider monkeys being better able to inhibit taking the food until the situation was favourable. The latter hypothesis is supported by a recent study showing that spider monkeys outperform capuchin monkeys and long-tailed macaques in a series of tasks measuring inhibitory control (Amici *et al.* 2008). In any case, capuchin monkeys' tactic was less efficient than that of spider monkeys, with the former obtaining less food overall.

Long-tailed macaques showed the lowest number of attempts at retrieving food in the experimental condition, and when attempts occurred, they almost always happened when the dominant was far from the box, showing considerable restraint. Such a good level of inhibition may seem to be at odds with previous studies, indicating that macaques perform worse than other primates in tasks requiring inhibition (Albiach-Serrano *et al.* 2007; Amici *et al.* 2008). One possible explanation is that although macaques perform relatively poorly in non-social-inhibition tasks, they might excel at inhibition in the social domain. Future studies should therefore design a battery of inhibitory tasks with a strong social component to evaluate possible different abilities for social and non-social inhibition. However, it is also conceivable that the restraint shown by spider monkeys and macaques is of a different nature. Long-tailed macaques may avoid the close proximity to dominants and 'freeze' their behavioural options in their presence. They may have low or no voluntary

control on certain behaviours in the presence of dominant partners—a trait that could be mediated by temperamental predispositions and reinforced by a history of aversive conditioning during social interactions. This is likely not to be characteristic of all macaque species given the interspecific variation in this genus (Thierry 2007). In contrast, spider monkeys do not freeze in the presence of dominant partners and can thus use behavioural options more flexibly. Thus, whereas spider monkeys could choose to approach the box depending on the circumstances, long-tailed macaques might not even face that choice.

As predicted, interspecific differences in the strictness of the dominance hierarchy differentially affected subordinates' behaviour. In long-tailed macaques, characterized by a strict dominance hierarchy, subordinates were so intimidated by the presence of the dominant to completely refrain from retrieving food in most cases. In contrast, spider monkeys and capuchin monkeys, with more relaxed dominance hierarchies, were less intimidated by the dominant. Additionally, species characterized by high levels of fission–fusion dynamics, such as chimpanzees, bonobos, orang-utans and spider monkeys, are expected to show enhanced inhibitory skills and higher behavioural flexibility when compared with species living in more cohesive groups (Amici et al. 2008; Aureli et al. 2008). Thus, as predicted, these two socioecological aspects appeared to have contributed to the outcomes of the current study by influencing the subjects' responses in distinct ways. Whereas the strictness of the dominance hierarchy constrains the subjects' tendency to approach the box (thus setting long-tailed macaques apart from the other two species), the degree of fission–fusion dynamics may affect the subjects' tendency to wait for a favourable situation to take the food in the presence of a dominant individual (thus setting spider monkeys apart from capuchin monkeys).

This work was supported by the SEDSU project (contract number 012-984 NEST Pathfinder) and the INCORE project (contract number 043318), both funded by the European Community's Sixth Framework Programme (FP6/2002–2006). We thank Colleen Schaffner, Iber Rodriguez Castillo, Roberto Pacheco Mendez, Fernando Victoria Arceo, Liesbeth Sterck, Elisabetta Visalberghi and all the animal keepers at the three facilities for endless support and cooperation.

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