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Capuchins do cooperate: the advantage of an intuitive task

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We used a cooperative pulling task to examine proximate aspects of cooperation in captive brown capuchin monkeys, *Cebus apella*. Specifically, our goal was to determine whether capuchins can learn the contingency between their partner's participation in a task and its successful completion. We examined whether the monkeys visually monitored their partners and adjusted pulling behaviour according to their partner's presence. Results on five same-sex pairs of adults indicate that (1) elimination of visual contact between partners significantly decreased success, (2) subjects glanced at their partners significantly more in cooperative tests than in control tests in which no partner-assistance was needed, and (3) they pulled at significantly higher rates when their partner was present rather than absent. Therefore, in contrast to a previous report by Chalmeau et al. (1997, *Animal Behaviour*, **54**, 1215–1225), cooperating capuchins do seem able to take the role of their partner into account. However, the type of task used may be an important factor affecting the level of coordination achieved.

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Cooperative behaviour has been described in a wide range of taxa. Most studies and discussions of cooperation concern ultimate explanations, such as the evolution of cooperation through mutualism, kin selection, or reciprocal altruism (Hamilton 1964; Trivers 1971; Krebs & Davies 1993; Dugatkin 1997). Research into these evolutionary issues has been conducted on a taxonomically diverse range of species, including lions, *Panthera leo* (Grinnel et al. 1995), Florida scrub-jays, *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick 1984), black hamlet fish, *Hypoplectrus nigricans* (Fischer 1980), and vampire bats, *Desmodus rotundus* (Wilkinson 1984). Relatively few studies, however, have examined the proximate aspects of cooperation, such as the underlying cognitive mechanisms. This is despite the fact that it has been suggested that the advanced cognitive abilities of humans and other primates may in fact derive from the need for complex forms of cooperation as well as other complexities inherent to life in cohesive social groups (Jolly 1966; Kummer 1971; Trivers 1971; Humphrey 1976; de Waal 1982). Recently, primatologists have begun to consider the cognitive aspects of cooperation (de Waal & Luttrell 1988; Boesch & Boesch 1989; Cheney & Seyfarth 1990; Chalmeau et al. 1997; de Waal 1997a, b, 2000; de Waal & Berger 2000).

Boesch & Boesch (1989) analysed chimpanzee (*Pan troglodytes*) hunting behaviour, suggesting four different levels of cooperation ranging from simple synchronous action to a division of labour among the hunters. There are obvious difficulties, however, in assessing the cognitive level at which individuals are operating in a field setting without control over critical variables. Assessing hunting in white-faced capuchins, *Cebus capucinus*, Rose (1997) notes the difficulty in obtaining sample sizes of hunts that could be adequately observed, and felt that apparent cases of collaboration could also be interpreted as individual opportunism. This reflection is reminiscent of the controversy that surrounded agonistic coalitions by baboon males, which were also suggested to be more self-serving than originally thought (Bercovitch 1988; Noë 1990). Experimental studies allow for more controlled and complete data collection of cooperative behaviour. Laboratory experiments in this field go back to work on chimpanzees in the Yerkes laboratories by Nissen & Crawford (1932), Crawford (1937) and Yerkes (1943).

A number of characteristics make capuchin monkeys (*Cebus* spp.) particularly suitable for a cooperation study. They show high levels of social tolerance, particularly with reference to food. Wild capuchin adults are tolerant of infants and juveniles while feeding (Izawa 1980; Janson 1988), and in captive studies adults have also been shown to be willing to share food with other adults (de Waal et al. 1993; de Waal 1997b). Capuchins are also highly dexterous, as evidenced by their use of tools in captivity (Visalberghi 1987; Anderson 1990) and their handling of food sources in the wild, such as the cracking of palm fruits and extraction of frogs from bamboo

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hollows (Izawa & Mizuno 1977; Izawa 1978). White-faced capuchins are known to hunt as a group for vertebrate prey and to share food afterwards (Rose 1997), although it is unclear if these hunts constitute cooperation on a level higher than what Boesch & Boesch (1989) label 'similarity': performance of the same action by two or more individuals without coordination in time or space.

In a recent study, Chalmeau et al. (1997) evaluated the performance of brown capuchin monkeys, *Cebus apella*, on a cooperative task. Individual subjects were first trained to pull one handle, then two, to activate the release of a food reward. The handles were connected to an electronic device that released the reward through an opaque tube. Eventually, the handles were moved far enough apart that one monkey could not reach both, and two monkeys had to simultaneously pull in order to be rewarded. The authors concluded that success at the task resulted only from chance co-occurrence of pulls by two subjects, and that the monkeys did not take into account the behaviour of the other pulling individual. They were therefore considered to operate on the level of 'similarity'. Negative results are hard to interpret, however, and several aspects of this study may have made a higher level of cooperation difficult to demonstrate. The tests were run such that the cooperation apparatus was freely available to all individuals in the group, which allowed for the monopolization of both the apparatus and the rewards by dominant animals. This may have reduced the cooperative motivation of some individuals. Furthermore, because the food release was electronically mediated, the task may not have been intuitively understandable to the monkeys. In the present study, we presented the same species with a more intuitive task under more controlled conditions to determine whether under such circumstances there is evidence for a higher level of cooperation.

Inspired by Crawford's (1937) classic experiment in which chimpanzees could collectively pull a box with food within reach, we designed a task in which two monkeys needed to work together to obtain a food reward. Only one of them would receive the food, but he or she had the opportunity to share the reward with the helper. This task was designed to study whether capuchins share food in exchange for received assistance (de Waal & Berger 2000). Earlier studies had shown that brown capuchins are willing to share food through mesh, and that sharing is reciprocal both across individuals and across time between any two individuals (de Waal et al. 1993; de Waal 1997b, 2000).

The present experiment involved presenting two capuchins, separated by a mesh partition, with food that could be brought within reach if both individuals simultaneously pulled on bars. Rather than allow all individuals access to the apparatus at once, we designated pairs of monkeys and tested them separately from the rest of the group. Also, our cooperation task was distinctly asymmetrical, not in action but in reward acquisition. Each individual in a pair served in the roles of recipient of the food reward and unrewarded helper on alternating occasions. This set-up, along with the use of the mesh partition, prevented any monopolization by dominant individuals and thereby allowed for data on every individual in the roles of food recipient and helper.

As in the Chalmeau et al. (1997) study, success in this task does require cooperation, but it does not necessarily demonstrate an 'understanding' of this condition by the subjects. That is, simultaneous pulls by the subjects may occur whether or not they have learned the need for synchronization. We tested several predictions to determine whether our subjects were taking into account their partner's actions. First, we recorded the rate of visual monitoring of the partner during pull attempts. We compared rates of glancing at the partner by individual 1 (the food recipient) in cooperation tests with that in solitary effort control tests in which the cooperation of individual 2 was not needed. In the former situation, when individual 1 needs its partner's help, one would predict a higher rate of visual monitoring. Next, we examined the influence of visual contact. If success in the task involves accounting for the partner's behaviour, rather than chance simultaneous pulling, one would predict the success rate to drop when visual contact is prevented. We therefore compared the success rate in the cooperation tests with the success rate in a modification of the test in which the monkeys had no visual contact.

We also examined whether the monkeys adjusted their actions to coincide with those of their partners. Cooperation studies in chimpanzees (Chalmeau 1994; Chalmeau & Gallo 1996) have suggested that some individuals learn to wait until a partner is present before attempting tasks that require cooperation. In a variation of the usual test set-up, we ran tests in which individual 1 was confined to its own section of the test chamber while individual 2 was free to enter or leave the other section of the chamber. As noted by Chalmeau et al. (1997), subjects that understand the partner's role would be expected to increase pulling activity when the partner is present (i.e. when cooperation is possible). Whereas these authors report that the 'frequency' of pulls made by subjects was unaffected by whether another individual was close to the apparatus or not, they failed to control for the amount of time that other individuals spent in or out of proximity. Pulling 'rates' (i.e. frequencies corrected for the relative duration of the two conditions) are the only informative measure. We examined the rate of pulling as a function of whether individual 2 was in or out of the test chamber.

METHODS

Subjects and Housing

Subjects were adults from two social groups of *C. apella* (designated the 'Nuts' and the 'Bolts') housed at the Yerkes Regional Primate Research Center since 1991. When testing began, one group (Bolts) had two adult males, five adult females, one subadult and six juveniles. The second group (Nuts) consisted of two adult males, five adult females, two subadults and seven juveniles. Five infants were born to each group over the course of the study (1998–1999). The monkeys were housed in indoor–outdoor pens, with one group (Bolts) having 25 m^2 total and the other (Nuts) having 31 m^2 total. The outdoor

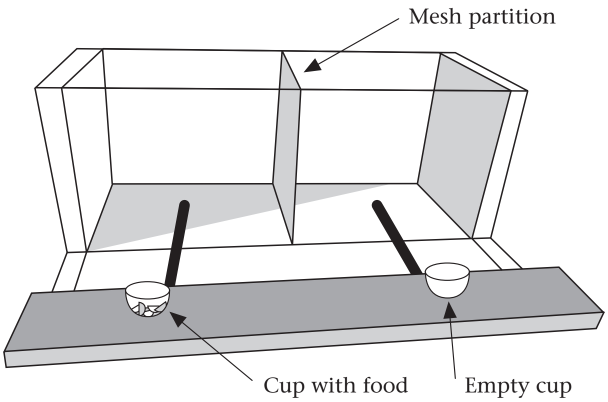

Figure 1. Two monkeys were situated in adjacent sections of the test chamber with a mesh partition between them. The apparatus consisted of a counter-weighted tray with two pull bars, each reaching into the test chamber of one partner. In cooperation tests (COP) the tray was too heavy for either one of the monkeys alone. The transparent cup for individual 1 was baited with apple pieces, whereas the transparent cup for individual 2 remained empty. In solitary effort tests (SOL), the bar for individual 2 was removed and the weight on the tray was reduced, thus decreasing the effort required by individual 1 to pull on its own. In obstructed view tests (OBS) the mesh partition was replaced by an opaque panel, which allowed both monkeys to see both cups but not each other.

sections were separated from the indoor sections by a wall, but two small doorways allowed the monkeys to move between the indoor and outdoor sections. Each indoor section was further divided into two sections by a chain-link fence, with two small (monkey-sized) doorways and one door accessible to people. The two social groups were visually separated by an opaque screen, but had auditory contact. The floors in each indoor pen were covered with wood chips. Monkey chow and water were available ad libitum and trays of fruit, vegetables, bread and protein juice were given to both groups each afternoon.

We only used same-sex adult pairs in the cooperation tests, and we always paired monkeys from the same social group. Subjects included two pairs from the Bolts group (one male–male, one female–female pair) and three pairs from the Nuts (one male–male, two female–female pairs).

Test Procedure

A test chamber measuring 144 × 60 × 60 cm was attached to the front of the indoor enclosure via a mesh tunnel. We removed individuals from their social group using a trained capture process; subjects entered a transport box and from there were moved to the test chamber. We then placed a mesh partition in the middle of the chamber, dividing it into two compartments measuring 72 × 60 × 60 cm. A plastic panel prevented movement from the test chamber back into the group cage until testing was over.

The test apparatus (Fig. 1) consisted of a counter-weighted tray that attached to the test chamber. Two metal pull bars were attached to the tray and extended ca. 10 cm into the test chamber. The bars were oriented one in front of each subject. The tray was in full view of the monkeys and supported two transparent food bowls, one in front of each individual.

Each pair initially had two or three 1-h sessions in which they were acclimated to the test chamber and the pulling apparatus. Once acclimated, training on the task began by first rewarding individuals for touching the bar, and later only for pulling the bar. After each subject had learned individually to pull the tray into the locked position, the monkeys were tested in pairs and the tray was counter-weighted according to the particular test type (see below).

Test sessions lasted 40 min each, divided into four 10-min trials. A trial began when a human experimenter dropped food (a quarter of an apple, cut into slices) into the food bowl of individual 1; individual 2's cup remained empty. Immediately after the food drop, the experimenter exited the area. The trials were recorded on Super-VHS by a remote-controlled video camera.

The monkeys could bring the food bowls within reach by pulling on the metal bars. Following a successful pull, the tray was released back into position by remote control and remained in place until the next food drop. We conducted tests in the late morning or early afternoon, before the monkeys had received their daily portion of fruit and vegetables. After testing, we returned the pair to its group. To avoid undue stress, we did not separate infants from their mothers when the mothers were tested. No individuals were tested more than once a day; most were tested a maximum of three times per week.

We conducted four test types. (1) Cooperation test (COP): we counter-weighted the tray such that neither individual could pull the food within reach on his/her own. A mesh partition separated the subjects, allowing visual, auditory and physical contact, as well as food transfers from individual 1 to individual 2. (2) Solitary effort test (SOL): this test differed from the cooperation test in that the tray was weighted such that individual 1 could pull the food within reach by itself. In addition, we removed individual 2's pull bar so that any success was clearly due to the efforts of individual 1 alone. A mesh partition separated the two monkeys. (3) Obstructed view test (OBS): we weighted the tray such that cooperation between both individuals was required to complete the task. This test differed from the cooperation test only in that an opaque panel was placed between the subjects in lieu of a mesh partition, thus eliminating visual contact. The panel had a small hole in the back so that the monkeys were aware of each other's presence, but this hole was located such that if both monkeys were close to the pull bars they could not see each other. Since the opaque panel did not extend beyond the front part of the cage, individual 2 could see individual 1's cup and the food that it contained. (4) Unrestricted cooperation test (UCP): we removed the plastic panel that normally kept the monkeys from leaving the test chamber and entering the group cage. This allowed individual 2 to move freely between the test chamber and the adjoining group cage (Fig. 2). Individual 1 was in the half of the test chamber that was distal to the cage entrance and therefore this individual was still restricted to its section of the test

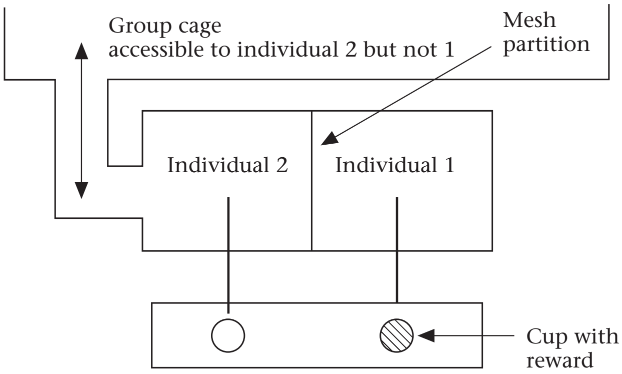

Figure 2. In unrestricted cooperation tests (UCP), individual 2 was free to move between the test chamber and the attached group cage. Individual 1 was still constrained to the test chamber by the mesh partition separating the two subjects. The rest of the group was in the outdoor section of the enclosure and could not interact with individual 2. The tray was weighted as in regular cooperation tests (COP), requiring the effort of both individuals.

chamber by means of the mesh partition separating the two monkeys. All other monkeys were moved to the outdoor cage during these tests, preventing interaction with individual 2. As in the cooperation tests, we weighted the tray such that both individuals needed to pull together for success.

We routinely conducted strength tests for each individual to determine the appropriate weight of the tray for each test type. All four trials in each test were of the same type. Each pair had a minimum of four tests (16 trials) of each test type.

Data Collection and Analyses

We recorded the success of the trials while tests were in progress. All other data were later coded from the videotapes. For COP, SOL and OBS tests, we recorded bar pulls (both successful and unsuccessful) by either or both individuals on an all-occurrence basis over the entire 10 min of each trial. In order for an action to be classified as a pull, it required exertion of force on the pull bar towards the subject (i.e. mere bar touches or pushing of the bar did not count as pulls). We recorded data on glancing from the time of the food drop until the food was obtained or the pull attempt aborted. Glances were defined as abrupt head movements in the direction of the partner lasting 1 s or less. When coding UCP tests, we marked a new time interval each time the location (in or out of the test chamber) of individual 2 changed. We recorded the duration of each interval and the number of pull attempts, defined above, by individual 1 during each interval.

We tested the agreement of the pulling and glancing observations (recorded by K.A.M.) with those of a student assistant unfamiliar with the experimental hypotheses. For a subset of the videotaped tests (three of each test type, for a total of 12 tests or 48 trials), K.A.M. and the assistant recorded the occurrence of pulls and glances in 5-s intervals for the first 1-min period of each trial. We then calculated Cohen's kappa to assess agreement of the two sets of observations and followed the procedure outlined by Bakeman & Gottman (1997) to determine whether the agreement differed significantly from chance.

All analyses respected individual variation, considering the behaviour of individual subjects under various conditions. We noted that the motivation of the subjects seemed to drop over the course of a test, decreasing in the later trials. We therefore analysed data on success rates and pulling rates using repeated measures analysis of variance (ANOVA) with trial number treated as an additional factor. As mentioned above, data on glancing were recorded during pull attempts and so are only available from those trials in which subjects were sufficiently motivated to pull. As a result, data were not available from all individuals to run repeated measures ANOVAs with trial as a second factor for glancing. For this measure, we therefore first ran a repeated measures test using the available data to confirm that there was no trial effect, and then collapsed the data across trials so that we could use data from all subjects.

As recommended by Keppel (1991), for each data set analysed with an ANOVA we conducted a Brown–Forsythe test for homogeneity of variance and a Geisser–Greenhouse correction to account for the sphericity assumption of repeated measures ANOVAs. For two of the data sets (pulling rates in COP versus OBS and pulling rates by individual 1 as a function of the location of individual 2) the assumption of homogeneity of variance was violated. As this violation increases the likelihood of type I error, Keppel (1991) recommends adopting a significance level of 0.025 when this assumption is violated. All significant results remained significant after this adjustment. Unless otherwise noted, all significant results also remained significant after the Geisser–Greenhouse correction. We conducted statistical analyses using SPSS 8.0.

RESULTS

Interobserver Agreement

The subset of 48 trials coded made for a total of 576 5-s intervals for pulls and 432 intervals for glances (there are fewer for glances as glances were not recorded in obstructed view tests). The observed agreement was 92.4% for pulls and 91.4% for glances. For both measures, agreement was significantly better than chance (pulls: $\kappa=0.6749$, $z=16.44$, $P<0.001$; glances: $\kappa=0.5926$, $z=12.32$, $P<0.001$). These values of kappa fall into ranges classified by Fleiss (1981) as 'good' and 'fair' for pulls and glances, respectively.

Visual Monitoring

The two-way repeated measures ANOVA revealed no effect of trial number on glancing rate ($F_{3,15}=1.091$, $P=0.383$, nondirectional). Hence data were combined across trials and a paired *t* test was applied to the combined data. Figure 3 shows the mean glancing rate

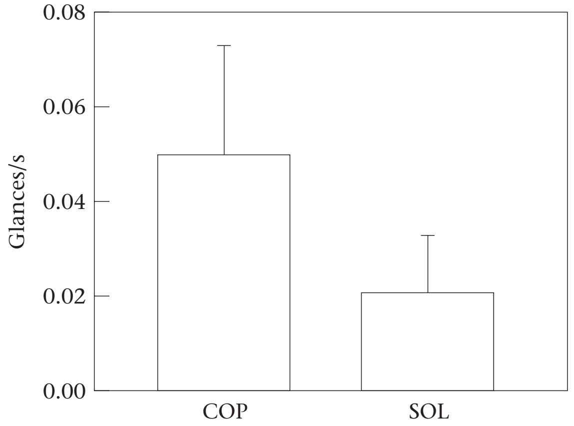

Figure 3. Mean+SE number of glances per second by individual 1 (the rewarded individual) towards individual 2 during pull attempts in cooperation tests (COP) and solitary effort tests (SOL). Data from all trials are combined.

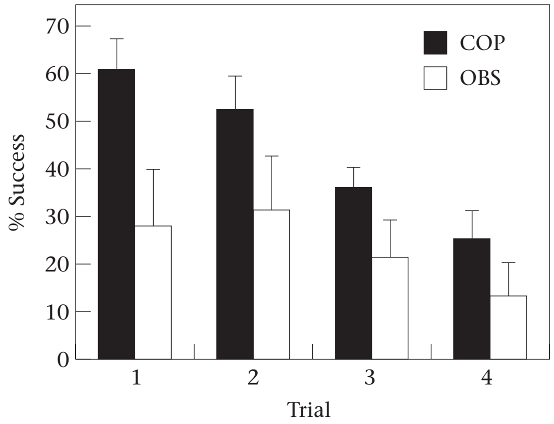

Figure 4. Mean+SE success rate in standard cooperation tests (COP), in which the partners had visual contact, and in obstructed view cooperation tests (OBS), in which there was no visual contact between partners. Data are presented separately for the four trials per test.

(glances/s) during pull attempts by individual 1 towards 2 in cooperation (COP) and solitary effort (SOL) tests. Individual 1 glanced more often at its partner in cooperative tests, when assistance was needed, than under the solitary effort condition (paired *t* test: $t_9=2.219$, $P=0.027$, one-tailed).

The Effect of Obstructing Visual Contact on Success

Figure 4 shows the percentage of successful cooperation (COP) and obstructed view (OBS) tests. As predicted, the success rate was higher in cooperative tests than in obstructed view tests, and success decreased over the course of trials (repeated measures ANOVA: test type: $F_{1,9}=6.625$, $P=0.015$, directional; trial: $F_{3,27}=5.782$, $P=0.0015$, directional). There was no test type by trial interaction ($F_{3,27}=1.252$, $P=0.311$, nondirectional).

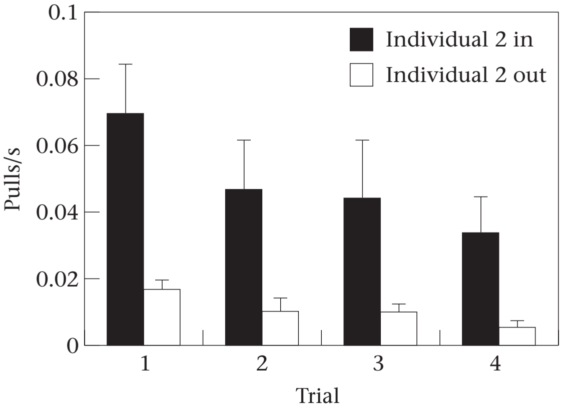

Figure 5. Mean+SE bar pulls per second for individual 1 (the rewarded individual) in unrestricted cooperation tests (UCP), in which individual 2 was free to move in and out of the test chamber. Pulling rates when individual 2 was in the test chamber are compared to pulling rates when individual 2 was out of the test chamber. Data are presented separately for the four trials per test.

The drop in success rate in the obstructed view test could result from either (1) an inability of the monkeys to coordinate pulls, or (2) a decreased pulling rate by one or both individuals under this condition. In support of the first hypothesis, an analysis of bar pulling by both individuals revealed no significant difference between pulling rates in cooperative versus obstructed view tests (repeated measures ANOVA: test type: $F_{1,9}=0.001$, $P=0.981$, nondirectional). Trial number and subject role (food recipient or helper) affected pulling rates as one might expect: pulling rates decreased over trials, and individuals pulled at a greater rate when in the role of individual 1 (food recipient) than when in the role of individual 2 (helper) (repeated measures ANOVA: trial: $F_{3,27}=18.269$, $P<0.001$, directional; subject role: $F_{1,9}=50.13$, $P<0.001$, directional). There was also a significant interaction between trial and subject role; that is, the decrease in pull rate over trials was greater in individual 2 than in individual 1 ($F_{3,27}=4.029$, $P=0.017$, nondirectional). However, this interaction was not significant after the Geisser–Greenhouse correction was applied.

Pulling Rates and Partner Presence

Figure 5 shows the mean pulling rate (pulls/s) by individual 1 in unrestricted cooperation tests (UCP) as a function of whether individual 2 was inside or outside of the test chamber. Individual 1 did adjust its pulling rate according to the presence or absence of its partner. Individual 1 pulled at a significantly higher rate when individual 2 was in the chamber than when individual 2 was outside (repeated measures ANOVA: $F_{1,7}=14.961$, $P=0.003$, directional). The decrease in pulling rate over trials was significant ($F_{3,21}=2.924$, $P=0.029$, directional), but did not remain so after the Geisser–Greenhouse correction. There was no significant interaction between trial and individual 2's location ($F_{3,21}=0.915$, $P=0.451$, nondirectional).

DISCUSSION

Contrary to a previous suggestion that cooperation among brown capuchin monkeys may merely be chance co-occurrence of individual actions (Chalmeau et al. 1997), the above results demonstrate that this species is able to learn certain aspects of their respective partners' roles in a cooperative task. The central piece of evidence is that the capuchins were significantly less successful in completing the task when visual contact between them was blocked. They did not pull less under this condition, but nevertheless succeeded less often, suggesting that coordination, not motivation, was the issue. In addition, in tests in which the partner's assistance was required, individual 1 (the individual to obtain the reward) glanced more often at the partner than in tests in which the partner's help was not needed, suggesting that individual 1 was monitoring its partner's behaviour. It is interesting to note, however, that the glancing behaviour observed in these tests has also been described as a mechanism of recruitment for agonistic support in this species (Freese & Oppenheimer 1981). The relationship between glancing rate and the need for assistance may reflect a solicitation function of glancing in addition to, or instead of, a monitoring function. Finally, in tests in which the helper was free to enter and exit the test chamber, pulling activity was adjusted to partner presence. It is therefore hard to maintain that success in this task was achieved through random action without regard of the partner's actions.

These findings present a considerably more complex picture of the cooperative abilities of capuchins than suggested by Chalmeau et al. (1997). As noted, the results of Chalmeau et al.'s study might have been different with more stringent controls in both the test paradigm and the statistical analysis. However, recent research in our own laboratory, using a task similar to that of Chalmeau et al. (1997), suggests that the nature of the cooperation task itself might have a significant effect on the results. In this study, capuchins were required to press levers to receive a juice reward. Individual capuchins quickly learned to press one lever for juice, but only one pair succeeded in the cooperative phase of the task, in which both individuals had to simultaneously press levers to obtain juice. In contrast to the present study, however, this pair's success rate was unaffected when visual contact between them was blocked, and neither individual adjusted its pressing behaviour in response to the partner's position relative to its lever. Thus, there appeared to be little or no consideration of the partner's behaviour (Brosnan & de Waal 2000; M. Campbell, unpublished data).

The monkeys' difficulty in understanding the cooperative nature of the pressing task may be two-fold. First, pressing a lever to receive juice delivered by an electronic device is neither transparent nor intuitive; there is no equivalent to such resource acquisition in the natural habitat of these monkeys. Second, the design of the apparatus allowed for a high rate of chance simultaneous lever-presses; learning of the required synchrony of actions was not required to achieve high rates of success. Both issues probably also apply to the apparatus of Chalmeau et al. (1997).

In contrast, subjects in the present study had to pull food directly towards themselves, a task for which the cause and effect relationship is probably immediately obvious to the monkeys; pulling food towards the self is a natural behavioural response. Additionally, chance success was prevented by the fact that it was a weighted task requiring exertion by both subjects at the same time; a high success rate was therefore more dependent on having learned the need for synchronous pulls. If one partner failed to pull, or released the bar too early, this could immediately be felt by the other, making for kinesthetic experiences conducive to learning the interindividual contingencies and understanding the cooperative nature of the task.

It is important to note that the word 'understanding' is used somewhat loosely here. It certainly cannot be assumed that the monkeys truly understand 'why' they are unable to complete a task when pulling alone but are able to when their partner performs the same action. Perhaps they simply learned the contingency between the co-occurrence of their actions and reward. However, given the test schedule applied, such a simple contingency would not work. One must keep in mind that the subjects had only four trials per session, at most three sessions per week, and that solitary effort controls were interspersed with the cooperation tests. If they learned a contingency, it would have to have been something more complex, such as 'if pulling alone does not work, only pulling when the partner is present will result in reward'.

Capuchins, then, seem capable of cooperation on a level thus far attributed to chimpanzees (Chalmeau 1994) but not macaques (Petit et al. 1992). This could result from either a higher level of social tolerance in capuchins relative to macaques, or from the lack of comparable systematic testing of macaques. One should not, however, rule out the third possibility that the demonstrated abilities reflect a different or greater role of cooperation in the lives of wild capuchins. Cooperation may yet prove to be an important component of capuchin hunting (Rose 1997) as it appears to be for chimpanzees (Boesch & Boesch 1989). If so, the task used in the present study, with its requirement of cooperation for a reward obtained by only one of the cooperators, may not only have the advantage of being intuitive, but also of being ecologically valid in some of its basic contingencies.

Acknowledgments

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References

Anderson, J. R. 1990. Use of objects as hammers to open nuts by capuchin monkeys (*Cebus apella*). *Folia primatologica*, **54**, 138–145.

Bakeman, R. & Gottman, J. M. 1997. *Observing Interaction: an Introduction to Sequential Analysis*. 2nd edn. Cambridge: Cambridge University Press.

Bercovitch, F. B. 1988. Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour*, **36**, 1198–1209.

Boesch, C. & Boesch, H. 1989. Hunting behaviour of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, **78**, 547–573.

Brosnan, S. F. & de Waal, F. B. M. In press. Variations on tit for tat: proximate mechanisms of cooperation and reciprocity. In: *Animal Cooperation* (Ed. by C. Boesch & M. Tomasello). Oxford: Oxford University Press.

Chalmeau, R. 1994. Do chimpanzees cooperate in a learning task? *Primates*, **35**, 385–392.

Chalmeau, R. & Gallo, A. 1996. What chimpanzees (*Pan troglodytes*) learn in a cooperative task. *Primates*, **37**, 39–47.

Chalmeau, R., Visalberghi, E. & Gallo, A. 1997. Capuchin monkeys (*Cebus apella*) fail to understand a cooperative task. *Animal Behaviour*, **54**, 1215–1225.

Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys See the World*. Chicago: University of Chicago Press.

Crawford, M. P. 1937. The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs*, **14**, 1–88.

Dugatkin, L. A. 1997. *Cooperation Among Animals*. New York: Oxford University Press.

Fischer, E. A. 1980. The relationship between mating system and simultaneous hermaphroditism in the coral reef fish, *Hypoplectrus nigricans*. *Animal Behaviour*, **28**, 620–633.

Fleiss, J. L. 1981. *Statistical Methods for Rates and Proportions*. New York: J. Wiley.

Freese, C. H. & Oppenheimer, J. R. 1981. The capuchin monkeys, genus *Cebus*. In: *Ecology and Behavior of Neotropical Primates. Vol. 1* (Ed. by A. F. Coimbra-Filho & R. A. Mittermeier), pp. 331–390. Rio de Janeiro: Academia Brasileira de Ciências.

Grinnel, J., Packer, C. & Pusey, A. E. 1995. Cooperation in male lions: kinship, reciprocity, or mutualism? *Animal Behaviour*, **49**, 95–105.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology*, **7**, 1–52.

Humphrey, N. K. 1976. The social function of intellect. In: *Growing Points in Ethology* (Ed. by P. P. G. Bateson & R. A. Hinde), pp. 303–321. Cambridge: Cambridge University Press.

Izawa, K. 1978. Frog-eating behavior of wild black-capped capuchin (*Cebus apella*). *Primates*, **19**, 633–642.

Izawa, K. 1980. Social behavior of the wild black-capped capuchin (*Cebus apella*). *Primates*, **21**, 443–467.

Izawa, K. & Mizuno, A. 1977. Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). *Primates*, **18**, 773–792.

Janson, C. H. 1988. Food competition in brown capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. *Behaviour*, **105**, 53–76.

Jolly, A. 1966. Lemur social behavior and primate intelligence. *Science*, **153**, 501–506.

Keppel, G. 1991. *Design and Analysis: a Researcher's Handbook*. Englewood Cliffs, New Jersey: Prentice Hall.

Krebs, J. R. & Davies, N. B. 1993. *An Introduction to Behavioural Ecology*. 3rd edn. Oxford: Blackwell Scientific.

Kummer, H. 1971. *Primate Societies*. Chicago: Aldine.

Nissen, H. & Crawford, M. 1932. A preliminary study of food-sharing behavior in young chimpanzees. *Journal of Comparative Psychology*, **22**, 383–419.

Noë, R. 1990. A veto game played by baboons: a challenge to the use of the prisoner's dilemma as a paradigm for reciprocity and cooperation. *Animal Behaviour*, **39**, 78–90.

Petit, O., Desportes, C. & Thierry, B. 1992. Differential probability of 'coproduction' in two species of macaque (*Macaca tonkeana*, *Macaca mulatta*). *Ethology*, **90**, 107–120.

Rose, L. M. 1997. Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology*, **18**, 727–765.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35–57.

Visalberghi, E. 1987. Acquisition of nut-cracking behaviour by 2 capuchin monkeys (*Cebus apella*). *Folia primatologica*, **49**, 168–181.

de Waal, F. B. M. 1982. *Chimpanzee Politics: Power and Sex among Apes*. Baltimore, Maryland: Johns Hopkins University Press.

de Waal, F. B. M. 1997a. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, **18**, 1–12.

de Waal, F. B. M. 1997b. Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology*, **111**, 370–378.

de Waal, F. B. M. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, **60**, 253–261.

de Waal, F. B. M. & Luttrell, L. M. 1988. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethology and Sociobiology*, **9**, 101–118.

de Waal, F. B. M. & Berger, M. L. 2000. Payment for labour in monkeys. *Nature*, **404**, 563.

de Waal, F. B. M., Luttrell, L. M. & Canfield, M. E. 1993. Preliminary data on voluntary food sharing in brown capuchin monkeys. *American Journal of Primatology*, **29**, 73–78.

Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bat. *Nature*, **308**, 181–184.

Woolfenden, G. E. & Fitzpatrick, J. W. 1984. *The Florida Scrub Jay*. Princeton, New Jersey: Princeton University Press.

Yerkes, R. M. 1943. *Chimpanzees: a Laboratory Colony*. New Haven, Connecticut: Yale University Press.