biology letters
Animal behaviour

Biol. Lett.
doi:10.1098/rsbl.2008.0410
Published online

Helping behaviour and regard for others in capuchin monkeys (*Cebus apella*)

Jennifer L. Barnes*, Tyler Hill, Melanie Langer, Margaret Martinez and Laurie R. Santos

Department of Psychology, Yale University, New Haven, CT 06520, USA
**Author and address for correspondence: 2 Hillhouse Avenue, New Haven, CT 06520, USA (jennifer.barnes@yale.edu).*

Altruism is an evolutionary puzzle. To date, much debate has focused on whether helping others without regard to oneself is a uniquely human behaviour, with a variety of empirical studies demonstrating a lack of altruistic behaviour in chimpanzees even when the demands of behaving altruistically seem minimal. By contrast, a recent experiment has demonstrated that chimpanzees will help a human experimenter to obtain an out-of-reach object, irrespective of whether or not they are offered a reward for doing so, suggesting that the cognitions underlying altruistic behaviour may be highly sensitive to situational demands. Here, we examine the cognitive demands of other-regarding behaviour by testing the conditions under which primates more distantly related to humans—capuchin monkeys—help an experimenter to obtain an out-of-reach object. Like chimpanzees, capuchin monkeys helped human experimenters even in the absence of a reward, but capuchins systematically failed to take into account the perspective of others when they stood to obtain food for themselves. These results suggest an important role for perspective taking and inhibition in altruistic behaviour and seem to reflect a significant evolutionary development in the roots of altruism, and specifically in other-regarding behaviour, between the divergence of New World monkeys and apes.

Keywords: altruism; non-human primate; perspective taking; inhibition; comparative cognition

1. INTRODUCTION

Recent comparative research has painted a somewhat conflicting picture regarding the evolutionary roots of our own species' other-regarding behaviour. Unlike other primates (Burkart *et al.* 2007; Lakshminarayanan & Santos in press), chimpanzees show a lack of regard for others across a variety of experimental designs in which they fail to deliver food to others at no cost to themselves (Silk *et al* 2005; Jensen *et al.* 2006). By contrast, chimpanzees readily help a human experimenter to obtain a goal object even in costly situations and seemingly without regard for their own usage (Warneken & Tomasello 2006; Warneken *et al.* 2007).

This dichotomy of chimpanzee successes and failures at showing prosocial behaviour suggests that the cognitive processes involved in altruistic behaviour are highly sensitive to contextual demands. In order to identify and explore the cognitive and behavioural prerequisites that might underlie other-regarding behaviour, one would profit from designing an experimental situation that can engender both successes *and* failures in a single species so that the variables affecting performance can be analysed more directly.

We develop just such an experimental situation by adapting the out-of-reach-object paradigm (Warneken *et al.* 2007) for use with a more distantly related primate species, the capuchin monkey (*Cebus apella*). Despite being more distantly related to humans than chimpanzees, other apes and Old World monkeys, capuchins have occupied a special niche in studies investigating the evolution of prosociality and fairness (e.g. Brosnan & de Waal 2003; Dubreuil *et al.* 2006), in part owing to their species-specific willingness to share food with conspecifics (de Waal 2000). However, previous research has suggested that capuchins may have a more limited perspective-taking capacity than chimpanzees (Hare *et al.* 2000, 2003). Because behaving in the interest of others requires not only inhibiting acting in one's own best interest, but also looking for and recognizing the interests of others, it was hypothesized that capuchins might be less predisposed towards attending to the goals of a human experimenter and helping her to achieve those goals and might therefore behave differently from chimpanzees on this kind of helping task.

2. MATERIAL AND METHODS

(a) *Experiment 1*

(i) *Subjects*

Seven capuchin monkeys (six adults and one juvenile) participated in this experiment. An additional juvenile began the experiment, but data collection could not be completed due to experimental error. All subjects were group housed at the Comparative Cognition Laboratory at Yale University.

(ii) *Procedure*

We closely followed procedures previously used to test chimpanzees' helping behaviour (Warneken *et al.* 2007). At the beginning of each session, a monkey was isolated in a large cage, to which a cubic annex could be attached (see figure 1*a*). The subject watched as two human experimenters fought over a target object. The second experimenter ultimately obtained the object and placed it inside the annex cage such that the target object was now out of the reach of the first experimenter, but inside the reach of the subject monkey. In the *reach* conditions, the experimenter actively reached through the hole with her left hand, attempting repeatedly to grasp the object, which remained out of reach. In *no reach* conditions, the experimenter put her left hand through the hole in the annex wall, but made no attempt to reach the object, allowing her hand to dangle inside the annex. In both conditions, the experimenter held up her right hand. In *reward* conditions, she held a grape in this hand, offering the monkey a reward in exchange for the object. In *no reward* conditions, the experimenter's right hand remained empty. In all conditions, the experimenter looked intently at the object, alternating her gaze between the object and the subject.

Each subject received four sessions, presented in pseudo-randomized order: reach/reward; no reach/reward; reach/no reward; and no reach/no reward. Sessions consisted of ten 60 s trials. A subject was considered to have 'helped' on a trial if it picked up the target object and placed it in the experimenter's hand within the 60 s time window. If the monkey had not handed the target object to the experimenter within 30 s, the experimenter began calling to the monkey to draw its attention. All trials were videotaped by a Sony Handycam; due to a camera error, video footage for four sessions could not be recovered.

Received 22 July 2008
Accepted 2 September 2008

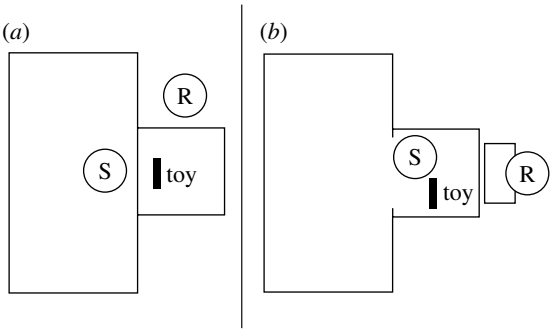

Figure 1. A representation of the experimental set-up in experiments (*a*) 1 and (*b*) 2. In both experiments the recipient human experimenter (R) reached for an out-of-reach toy which the subject monkey (S) could access.

Figure 2. Results of experiment 2. The percentage of capuchins' helping behaviour in a given session across reach/no reach and reward/no reward conditions.

(**b**) ***Experiment 2***

(iii) *Subjects*

Six capuchins completed experiment 2: five of the adults from experiment 1 and the juvenile male who was previously unable to complete experiment 1. Two additional subjects were excluded from analysis because they were unable to complete all four sessions.

(iv) *Procedure*

The procedure for experiment 2 was identical to that of experiment 1 except for a few changes. The grid that separated the testing cage from the annex was removed to allow monkeys to climb into the annex, where they could easily pick up and manipulate the four target objects. Because the monkeys were allowed into the annex in experiment 2, for the experimenter's safety and the monkey's comfort, the experimenter did not reach *into* the cage. Rather, a large table was placed in front of the annex, so that the experimenter was forced to try to reach over the table towards the target object, but was prevented by the table from being able to reach into the cage (see figure 1*b*).

3. RESULTS

In experiment 1, few capuchins demonstrated helping behaviour when required to reach outside their cage to manoeuvre the object into the experimenter's hand. Only two of the seven monkeys helped more than once across a total of 40 trials. These results directly contrast with those found in chimpanzees, who demonstrated helping behaviour frequently, not only in this low-cost condition (see experiment 1 in Warneken *et al.* 2007), but also in more costly conditions which required climbing and manoeuvring extensively to retrieve the target object (see experiment 2 in Warneken *et al.* 2007). Capuchins' failure to help is especially surprising since capuchins in this population regularly obtain objects from outside their home cage and exchange them with human experimenters. A direct comparison with the chimpanzee data revealed that while the chimpanzees in the previous experiment helped at least once in 19 out of 36 ten-trial sessions (53% of the time), the capuchins helped only 4 out of 28 ten-trial sessions (14%).

In contrast to experiment 1, the low-cost set-up of experiment 2 successfully engendered capuchins' helping behaviour, with all six subjects repeatedly handing the target object to the experimenter across the four experimental sessions (see figure 2), allowing us to explore the roles that the presence or absence of a reward, and the presence or absence of an experimenter's reach towards the target object, played in the capuchins' willingness to help the experimenter obtain the object. We first explored whether capuchins, like chimpanzees, base their helping behaviour on whether or not the experimenter was reaching for the target object, regardless of whether a reward was offered in exchange for help. Contrary to this hypothesis, we found only a marginal effect of reaching ($F_{1,5}=4.57$, $p=0.09$). Instead, we observed that capuchins' helping behaviour is based more on the presence or absence of a reward, with capuchins' helping significantly more when a reward is present (mean=98.3% helping) than when it is absent (mean=45.8% helping, $F_{1,5}=29.1$, $p=0.003$). Our analysis also revealed a significant reach by reward interaction ($F_{1.5}=7.48$, $p=0.04$), such that capuchins care little about an experimenter's reaching behaviour in the presence of a reward ($t(5)=0.0$, $p=$n.s., one-tailed), but base their helping behaviour on this cue in the absence of a reward ($t(5)=2.48$, $p=0.03$, one-tailed). We also observed that most acts of helping happened quickly; only 7 per cent of helping acts occurred after the 30 s mark.

4. DISCUSSION

Taken together, the results of experiments 1 and 2 show important species differences in helping behaviour. In comparison with chimpanzees, capuchin monkeys seem somewhat stuck on their own personal pay-offs, paying more attention both to the potential costs and to the potential benefits of helping. In experiment 1, in which the costs of helping were relatively high, very few capuchins spontaneously helped a human experimenter to obtain an out-of-reach object. While chimpanzees demonstrate helping behaviour even at great cost to themselves (Warneken *et al.* 2007), the capuchins in our experiment seem to be very sensitive to the amount of effort required to help. These results provide an interesting complement to previous research, in which capuchins' sensitivity to fairness and the degree to which they showed inequity aversion was moderated by the amount of effort they were required to expend to receive 'fair' or 'unfair' rewards (Brosnan & de Waal 2003; Van Wolkenten *et al.* 2007). Unlike chimpanzees, capuchins seem to be uniquely cued into the amount of effort an action requires, and they seem to prioritize the potential cost to themselves over the potential benefit to the individual in need of help.

When helping required minimal effort in experiment 2, capuchins seemed to pay a great deal of attention to their own potential benefits, rather than

the benefit that their actions could deliver to the experimenter. While chimpanzees in a previous experiment based their helping behaviour primarily on whether or not an experimenter demonstrated a desire for the object by reaching for it, capuchins based their helping behaviour first and foremost on the presence or absence of a reward and only considered the experimenter's goal-oriented reaching behaviour when they did not stand to gain from helping themselves. In other words, while the capuchins did show regard for others, they did so in a restricted sense, concentrating first and foremost on their own potential gain and only secondarily on the desires of others. It is possible that when capuchins helped in the absence of a reward, they did so because they thought there was some chance of being rewarded; however, it should be noted that when no reward was offered, capuchins based their helping behaviour on the experimenter's reach, even though this cue itself was not specifically associated with reward in this or previous experiments.

These results suggest that while capuchins may be *capable* of showing regard for others, there may be important phylogenetic differences in the constraints under which they actually do so, with a possible divergence between New World monkey species and apes with regard to their ability to see past or inhibit acting in one's own best interest in order to provide a benefit to others. Our results suggest that certain cognitions, such as perspective taking, may allow a species to overcome a predisposition towards acting with self-regard. In addition to constituting an important species difference *within* the primate order, these capacities may be highly sensitive to contextual demands, particularly in tasks in which food retrieval is involved, or in which the signals to another's goals are less salient. Future research may thus profit from examining how prosocial capacities vary across experimental contexts in order to illuminate the role that socio-ecological factors may play in this phylogenetic distinction.

This research conforms to the guidelines for use of animals in research and was approved by the Yale University IACUC.

The authors would like to thank Kerstin Frailey and Rebecca Fabbro for their help with running this experiment and Dr Felix Warneken and his collaborators for their helpful advice and for allowing us to use the original chimpanzee dataset.

Brosnan, S. & de Waal, F. B. M. 2003 Monkeys reject unequal pay. *Nature* **425**, 197–199. (doi:10.1038/nature01963)

Burkart, J., Fehr, E., Efferson, C. & Van Schaik, C. 2007 Other-regarding preferences in a non-human primate: common marmosets provide food altruistically. *Proc. Natl Acad. Sci.* **104**, 19 762–19 766. (doi:10.1073/pnas.0710310104)

de Waal, F. B. M. 2000 Attitudinal reciprocity in food sharing among brown capuchins. *Anim. Behav.* **60**, 253–261. (doi:10.1006/anbe.2000.1471)

Dubreuil, D., Gentile, M. S. & Visalberghi, E. 2006 Are capuchin monkeys (*Cebus apella*) inequity averse? *Proc. R. Soc. B* **273**, 1223–1228. (doi:10.1098/rspb.2005.3433)

Hare, B., Call, J., Agnetta, B. & Tomasello, M. 2000 Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* **59**, 771–785. (doi:10.1006/anbe.1999.1377)

Hare, B., Addessi, E., Call, J., Tomasello, M. & Visalberghi, E. 2003 Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Anim. Behav.* **65**, 131–142. (doi:10.1006/anbe.2002.2017)

Jensen, K., Hare, B., Call, J. & Tomasello, M. 2006 What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proc. R. Soc. B* **273**, 1013–1102. (doi:10.1098/rspb.2005.3417)

Lakshminarayanan, V. R. & Santos, L. R. In press. Capuchin monkeys are sensitive to others' welfare. *Curr. Biol.*

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., Lambeth, S. P., Mascaro, J. & Schapiro, S. J. 2005 Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* **437**, 1357–1359. (doi:10.1038/nature04243)

Van Wolkenten, M., Brosnan, S. F. & de Waal, F. B. M. 2007 Inequity responses of monkeys modified by effort. *Proc. Natl Acad. Sci.* **104**, 18 855–18 859. (doi:10.1073/pnas.0707182104)

Warneken, F. & Tomasello, M. 2006 Altruistic helping in human infants and young chimpanzees. *Science* **311**, 1301–1303. (doi:10.1126/science.1121448)

Warneken, F., Hare, B., Melis, A. P., Hanus, D. & Tomasello, M. 2007 Spontaneous altruism by chimpanzees and young children. *PLOS Biol.* **5**, 1414–1420. (doi:10.1371/journal.pbio.0050184)