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Capuchins' (*Cebus apella*) sensitivity to others' goal-directed actions in a helping context

Lindsey A. Drayton · Laurie R. Santos

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Abstract As humans, our ability to help others effectively is at least in part dependent upon our capacity to infer others' goals in a variety of different contexts. Several species of nonhuman primate have demonstrated that they will also help others in some relatively simple situations, but it is not always clear whether this helping is based on an understanding of another agent's goals. Although the results of a number of different studies support the hypothesis that chimpanzees represent others' goals in various helping contexts and are sensitive to these goals when actually helping others, less work has addressed whether more distantly related species actively represent goals when helping. To explore the cognitive mechanisms underlying helping behaviors in species less closely related to humans, we tested whether a species of New World monkey—the brown capuchin (*Cebus apella*)—would provide an experimenter with a desired out-of-reach object more often than an alternative object when the experimenter attempted to obtain the former object only. We found that capuchins reliably helped by providing the experimenter's goal object (Experiment 1) and that explanations based on the use of several less sophisticated strategies did not account for the overall pattern of data (Experiments 2–4). Results are thus consistent with the hypothesis that capuchins help others based on an understanding of their goals although more work is needed to address the possibility that capuchins may be responding to gestural and postural factors alone.

L. A. Drayton (✉) · L. R. Santos
Psychology Department, Yale University, 2 Hillhouse Avenue, New Haven, CT 06511, USA
e-mail: lindsey.drayton@yale.edu

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Introduction

In human societies, individuals regularly help others achieve their goals. This kind of altruistic behavior is often referred to as instrumental helping and relies on a combination of cognitive and motivational factors (Warneken and Tomasello 2009). From a cognitive standpoint, a helper must be able to infer another person's goal and understand how to best assist them. From a motivational standpoint, a helper must be willing to engage in a potentially costly behavior that produces no immediate benefits. Human adults are exceptional helpers in both of these respects. Even in the absence of explicit external cues, we are able to mentally represent others' situation specific goals and desires by intentionally simulating what we ourselves might experience in a similar situation (e.g., Mitchell 2009). These kinds of uniquely human cognitive abilities likely interact with species-specific motivational mechanisms, such as the desire to adhere to social norms or sensitivity to reputation formation (Fehr and Fischbacher 2003), to produce a range of altruistic behaviors not seen in the greater animal kingdom.

To fully understand the extent to which instrumental helping is a human-unique ability, it is necessary to explore whether other animals also help in ways that demonstrate that they are sensitive to others' goals. Although researchers have studied prosocial behaviors in a variety of species in recent years [e.g., bonobos (*Pan paniscus*): Hare and Kwetuenda 2010; Tan and Hare 2013; chimpanzees (*Pan troglodytes*): Horner et al. 2011; Jensen et al. 2006; Silk et al. 2005; Vonk et al. 2008; brown capuchins (*Cebus*

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apella): de Waal et al. 2008; Lakshminarayanan and Santos 2008; Takimoto et al. 2010; common marmosets (*Callithrix jacchus*): Burkart et al. 2007; cotton-top tamarins (*Saguinus oedipus*): Cronin et al. 2009, 2010; Stevens 2010; gray parrots (*Psittacus erithcus*): Péron et al. 2013; jackdaws (*Corvus monedula*): Schwab et al. 2012; long-tailed macaques (*Macaca fuscicularis*): Massen et al. 2010, 2011; ravens (*Corvus corax*): Di Lascio et al. 2013; rhesus macaques (*Macaca mulatta*): Chang et al. 2011], comparative psychologists have looked primarily to two primate species—chimpanzees and brown capuchin monkeys—to more carefully study the phylogeny of instrumental helping. In a landmark series of experiments, Warneken and colleagues found that when a human experimenter attempted to grasp an out-of-reach object, chimpanzees regularly helped the experimenter by retrieving the object (Warneken and Tomasello 2006; Warneken et al. 2007). In contrast, when a human experimenter simply looked at an object but did not reach toward it, chimpanzees were significantly less likely to help. Warneken and colleagues observed that chimpanzees continued to help even when doing so required substantially more physical effort and—perhaps most surprisingly—when they did not stand to gain any food rewards. Barnes et al. (2008) used a similar task to test helping performance in capuchin monkeys. Like Warneken et al. (2007), they varied the presence of a food reward and whether the experimenter reached toward the object. When no food was present, capuchins helped more often when the experimenter was reaching toward the object, but when food was present, capuchins provided the experimenter with the object on nearly all test trials regardless of whether a reaching cue was present or absent. In this way, capuchins differed from chimpanzees in that they were much more likely to help when a reward was present. Unlike chimpanzees, however, capuchins rarely helped when retrieving the object was made more difficult.

These results suggest that for both chimpanzees and capuchins, the act of seeing a person perform a goal-directed reach promotes instrumental helping in some contexts (see also Westergaard et al. 2007; Yamamoto et al. 2009). However, whereas chimpanzees may be motivated by the benefit that their helpful action imparts upon a partner, capuchins seem to act largely out of self-interest, at least in this particular testing environment. Additionally, to date, only chimpanzees have shown evidence of interpreting a person's reaching cues in a relatively flexible and complex manner. For example, Yamamoto et al. reported that chimpanzees were able to modify their helping behavior according to situational demands (Yamamoto et al. 2012). In their task, chimpanzee helpers were presented with a variety of different tools and could hand one of these tools to a conspecific partner facing a particular tool problem. Yamamoto et al. found that chimpanzees transferred only the appropriate tool to their partner, suggesting that they modified their helping behavior based on the particular needs of a given situation (for a conceptually related set of results, see Melis and Tomasello 2013).

These studies provide compelling evidence in support of the hypothesis that chimpanzees use representations of other individuals' goals to guide their patterns of helping. Unfortunately, it is less clear whether this ability is shared with more distantly related species of primate. On one hand, capuchin monkeys' behavior in Barnes et al. (2008) is consistent with the hypothesis that capuchins are sensitive to others' goals in a helping context even though they are not particularly motivated to help in the absence of an external reward. In addition, there is some experimental work suggesting that capuchins are sensitive to the intentions behind an agent's action (Phillips et al. 2009), which further supports the possibility that this species could potentially represent goals in the context of instrumental helping as well. On the other hand, it is possible to interpret Barnes et al.'s findings in a more deflationary way; perhaps the act of reaching simply drew capuchin subjects' attention to the desired object or highlighted the potential for a particular pattern of action (i.e., giving a human experimenter an object in exchange for food). This more deflationary alternative seems to be even more likely given that the population of capuchins that participated in the Barnes et al. study had previously been trained to return tokens presented on a tray to human experimenters in exchange for food rewards (e.g., Chen et al. 2006) and occasionally have been seen to offer various objects that they find in their home enclosure to experimenters without being solicited in any way (Drayton, personal observation). Thus, capuchins' behavior in the Barnes et al. helping task might not reflect sensitivity to the experimenter's goal, but might instead reflect a generally propensity to give humans objects in the hope of getting food.

In this series of studies, we hoped to at least take a first step toward distinguishing between these two alternatives. To do so, we extended the results of Barnes et al. (2008) by exploring whether capuchins' helping behavior in the out-of-reach object task can be explained by a number of low-level attentional spotlighting accounts. To do this, we modified the original Barnes et al. testing paradigm so that rather than only having one object available to give the experimenter, capuchin subjects had two candidate objects always available: a desired target object and a distractor object. As such, success on our task required not just that capuchins realize that the experimenter wanted an object, but instead, that the experimenter wanted *a particular object*. Critically, capuchin subjects were rewarded for returning either the target or distractor object to the experimenter. This ensured that the observed helping

behaviors were ones that subjects exhibited spontaneously rather than behaviors that were shaped over the course of our experiments through differential reinforcement. In this way, our new design was able to determine not just whether capuchins chose to help the experimenter but also the particular object they chose when helping.

In Experiments 1–3, we explored whether several different non-mentalistic attentional accounts could explain capuchins' performance in this new out-of-reach object task. Experiment 1 was designed to test whether seeing an experimenter reaching might make salient the option of providing the experimenter with an object. Experiments 2 and 3 explored whether seeing active reaching or mere hand proximity to a particular object might preferentially draw subjects' attention to the target object. Finally, in Experiment 4, we tested whether subjects might be adopting a minimally effortful strategy when choosing between the target and the distractor objects.

Note that our experiments were designed specifically to rule out the possibility that capuchins use a number of relatively simple strategies when deciding how to help others in an out-of-reach helping task. Although ruling out these simple strategies provides evidence that is consistent with the hypothesis that capuchins' helping is, like that of chimpanzees (Yamamoto et al. 2012), guided by goal representations, it is important to note that none of our experiments were designed to provide definitive evidence that capuchins were specifically representing others' goals in this task per se. For this reason, we have chosen to adopt non-mentalistic terminology (e.g., object-directed actions as opposed to goal-directed actions) throughout the paper when discussing both the logic and results of each experiment. However, we return to the important issue of whether capuchins' performance might in fact rely on more mentalistic goal representations later in the General Discussion.

Experiment 1

To explore whether seeing a person perform a reaching action might make salient the option of providing that person with an object generally, we first tested whether capuchins would give a target object to an experimenter more often than a distractor object when the experimenter reached toward and attempted to obtain the target object only. We reasoned that if reaching simply highlighted the potential for a particular pattern of action, that is, giving an experimenter an object in exchange for food, then capuchins should give target and distractor objects equally often. In contrast, if monkeys are sensitive to the fact that the experimenter's reaching action is specifically directed toward one object in particular, then capuchin subjects should give the target object to the experimenter more often than the distractor object.

Methods

Subjects

Eight brown capuchin monkeys (*C. apella*) participated in this study (Table 1). One additional capuchin was initially included but was dropped from the study after the first trial because she attempted to consume parts of the novel objects. All subjects were socially housed at the Comparative Cognition Laboratory at Yale University. Monkeys were fed twice daily on a diet of monkey chow, fruits, vegetables, and other snack items and had ad libitum access to water. Although monkeys were physically isolated during test sessions, they always had visual and auditory access to other group members. Some of the subjects had previously participated in Barnes et al. (2008), but no subject had participated in a helping study in which they had to choose which of two objects to give an experimenter.

Procedure

Subjects participated in two test sessions consisting of four trials each. At the start of each session, a monkey was isolated in a testing chamber. Attached to the testing chamber was a smaller (0.8 m^3) cube annex made of mesh caging. A schematic of the testing setup is shown in Fig. 1. The left and right side panels of the annex each had a hole (50 × 90 mm) embedded within the mesh (visible in Fig. 2). These holes were big enough to allow objects to be placed into the annex at the beginning of each trial. The front panel of the annex also had four (65 × 50 mm) holes embedded in the mesh (also visible in Fig. 2). These holes were big enough for all objects to fit through, but too small for a human hand to fit easily through. This setup enabled a human experimenter to convincingly attempt to obtain an

Table 1 Subject information

Subject	Sex	Age (years)[a]	Participated in
Auric Goldfinger	Male	16	Exp. 1–2, 4
Felix Leiter	Male	15	Exp. 1–4
Jill Masterson	Female	16	Exp. 1–4
Helga Brandt	Female	3	Exp. 1–4
Holly Goodhead	Female	11	Exp. 1–4
Honey Rider	Female	7	Exp. 1–4
Mayday	Female	10	Exp. 1–4
Nicknack	Male	16	Exp. 1–4

[a] At onset of Experiment 1

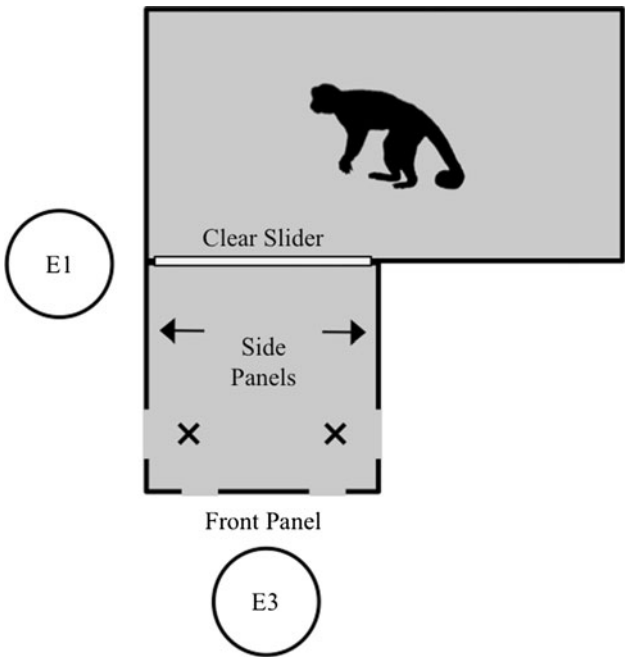

Fig. 1 Schematic of the testing setup used in Experiment 1. The figure depicts the setup after E2 has placed the target and distractor objects (represented by the two *cross marks*) into the annex and left the testing room. The subject has not yet been given access to the annex. Note the *two holes* in the *side panels* that allow E2 to place the objects into the annex, as well as the *holes* in the *front panel* through which E3 can attempt to obtain the target object. Experiments 2–4 all utilize similar testing setups (for detailed descriptions of differences see "Procedures" sections)

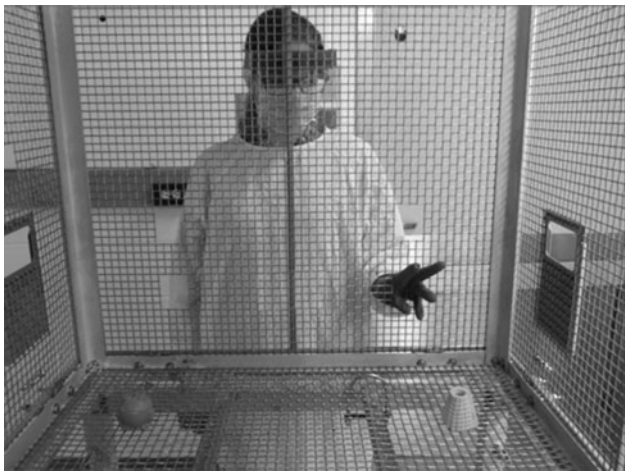

Fig. 2 Subjects' perspective upon entering the annex in Experiment 1. The target object is on the *right*

object through a hole in the front panel, but be genuinely unable to do so. A clear slider held in place by an experimenter (E1) prevented the subject monkey from entering the annex at will.

At the start of each trial, a second experimenter (E2) entered the testing room with two small novel objects (i.e., the target and the distractor object), one held in each hand. A third experimenter (E3) was also present in the testing room. Multiple experimenters were used to try to make salient the fact that one experimenter wanted but was unable to obtain an object that another experimenter had placed into the annex (see Barnes et al. 2008; Warneken et al. 2007 for similar procedures). After entering the room, E2 showed the subject the two objects and then placed them inside the annex, one on the right side and one on the left side. If the subject was not paying attention when the objects were presented, E2 would attempt to gain the subject's attention (e.g., by calling the subject's name). Inconspicuous marks on the floor of the annex indicated the exact placement of the objects, ensuring that the objects were placed in the same location on every trial. After placing the objects, E2 left the testing room. As soon as E2 left the room, E3, who had been watching this procedure, approached the annex. Once she was standing in front of the annex (at the horizontal midpoint of the front panel), she looked quickly at one objet and then at the other. She then reached partway inside the annex through one of the two lower holes in the front panel of the annex and attempted to obtain the target object by reaching toward it in a grasping gesture (Fig. 2). Approximately 10 s after E3 began reaching toward the target object, E1 removed the clear slider that was preventing the subject from entering the annex. E3 continued to reach toward the target object while alternating between looking at the target object and the subject. As soon as E3 received an object, she rewarded the subject with a single grape and exited the testing room. The trial ended if the subject did not give the experimenter an object within 60 s. If the subject gave both objects at the same time, the experimenter accepted both objects but still only gave the subject a single grape (this happened very rarely).

Four pairs of objects were used, and each pair was presented a single time within each session. The order in which object pairs were presented was randomized. Each of the eight objects served as the target object on a single trial. Which object within a given pair first acted as the target was counterbalanced across subjects, and the target object was located on the right and left side of the annex equally often.

Analysis

All trials were videotaped. Due to either experimenter or camera error, videos from four trials could not be recovered. Data from these trials were not included in any of the analyses. One additional trial was also discarded due to an experimenter error. From the videos, the object that the subject gave to the experimenter was recorded for each trial. Occasionally, a subject would appear to attempt to

give an object, but would fumble the object or pull it back inside the annex prior to releasing the object into the experimenter's hand and then proceed to give the experimenter the opposite object. For this reason, we also recorded which object subjects first attempted to give the experimenter on each trial. However, across all experiments reported, this "first attempt" measure led to the same results as measuring the object that subjects actually traded on each trial. For this reason, we present data based on the latter measurement only. Two coders independently coded all of the videos. Inter-rater reliability was high (Cohen's $\kappa = 0.90$), and a third coder resolved all disagreements. We calculated the percent of trials that each subject gave the target object as opposed to the distractor object on only a subset of trials. Trials on which the subject did not return either object ($n = 6$) or returned both objects at the same time ($n = 1$) were not included, leaving a total of 52 trials for analysis. One sample t tests were used to compare these percentages to chance levels. We also collapsed all subjects' data and used binomial tests to compare the total number of times that subjects as a group gave the target object to chance levels. All tests are two-tailed.

Results and discussion

Subjects gave the experimenter an object on the majority (90 %) of trials. Even though subjects could give either the target or the distractor object to the experimenter, they gave the target object at greater than chance levels ($M = 76$ %, $t_7 = 4.03$, $p = 0.005$; Fig. 3). A binomial test confirmed that subjects gave the target object significantly more often than chance ($p < 0.001$). At an individual level, six subjects gave the target object to the experimenter more often than the distractor object. Two subjects gave the target and distractor objects equally often. These results confirm the findings of Barnes et al. (2008) by showing that capuchins were perfectly willing to give an out-of-reach object to an experimenter when they received a reward for doing so. More interestingly, they go beyond this previous study to show that despite the fact that subjects were given the same reward for returning either object, subjects were significantly more likely to give the object that the experimenter was reaching toward and requesting over the alternative object.

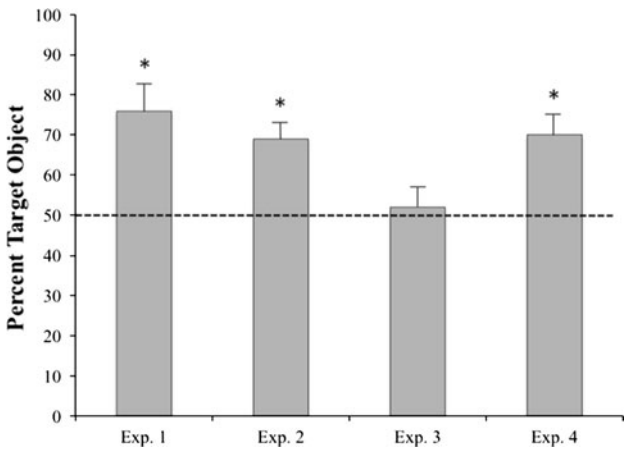

Fig. 3 Mean percent of trials (with standard errors) on which subjects gave the target object to the experimenter in Experiments 1–4. The *dashed line* shows the performance level (50 %) expected if subjects were responding randomly. *$p < 0.01$

Importantly, the results we observed here could not have been due to subjects' previous training or reinforcement history. As noted above, some of our subjects had previously been tested in the Barnes et al. (2008) study. Recall that in this study, subjects were sometimes given a food reward for giving an experimenter a requested object, but subjects also participated in an equal number of trials on which they were given a food reward for giving an object that was not requested, as well as trials on which they were given no food reward for giving a requested object. Our subjects' previous experience in this study makes it unlikely that subjects had learned that they would receive a food reward only for giving a requested object. In addition, our subjects have never been differentially reinforced for handing an experimenter one object over another. In this way, the results of Experiment 1 are unlikely to be due to subjects' previous reward history. Instead, subjects seem to connect a person's object-directed reaching with the particular object that she is requesting.

These results are noteworthy for several reasons. First, they suggest that capuchins do attend to a human experimenter's reaching cues and that they are able to do so in the presence of food. Thus, subjects' failure to differentiate between the reaching and non-reaching conditions in the presence of food in Barnes et al. (2008) was likely not due to a failure to attend to the presence or absence of a reaching action per se, but rather because subjects were highly motivated to engage in any behavior that might result in the acquisition of a reward. Second, capuchins' behavior was inconsistent with the hypothesis that reaching simply makes salient the option of providing the experimenter with *any object*. If this was the case, we would not expect the target object to be selected more often than the distractor object. Thus, these results provide evidence against at least one attentional spotlighting account of capuchins' performance on out-of-reach object tasks and are consistent with the hypothesis that capuchins were sensitive to the fact that the experimenter's action was directed at a particular object.

Experiment 2

Although our first experiment ruled out one attentional spotlighting account, capuchins' behavior could still be explained via several other alternative low-level accounts.

First, it is possible that subjects gave the target object more often in Experiment 1 because movement around that object (i.e., the experimenter's reaching action) preferentially drew their attention to the target object over the distractor object. To explore this, we ran a second experiment that followed the same general procedure as Experiment 1 with the exception that E3's behavior was altered. The most important change was that a static reaching cue was used. That is, the experimenter's arm was outstretched toward the target object, but she did not actively reach toward or attempt to obtain the target.

We reasoned that if subjects had been attracted only to the movement around the target object in the first study and had consequently given that object more often, then they would no longer distinguish between the target and distractor object when a static reaching action was employed. It is worth noting that although subjects' failure to give the target object more often would be consistent with the attentional spotlighting account described above, it would be equally consistent with the hypothesis that subjects represented the experimenter's actions as an object-directed only when she actively reached toward the target object. That is, active reaching may be an important cue to understanding another individual's behavior. Experiment 2 was not designed to test between these two very different interpretations, but because we were generally interested in the minimal set of cues that might be sufficient for the subjects to differentiate between the target and distractor objects, we further impoverished E3's actions by removing eye gaze and head orientation as possible sources of information. Conversely, if subjects did continue to give the target object more often even when this subtler reaching cue was used, then we could reject this second attentional spotlighting account. Success in Experiment 2 would mean that subjects could not be responding merely to movement around the target object. However, this pattern of performance would also be open to very different interpretations. On the one hand, this pattern of performance might indicate that subjects inferred that the experimenter's actions were object-directed despite the absence of an active reaching gesture or appropriate head orientation and eye gaze information. On the other hand, capuchins might simply be attracted to the object that was closer to the experimenter's hand (a possibility we will deal with in Experiment 3).

Methods

Subjects

The same eight capuchin subjects participated in this experiment.

Procedure

The procedure was similar to that of Experiment 1 with the exception that E3's reaching action was altered. Rather than looking first at both objects and then reaching inside the annex and attempting to grasp the target object, E3 gently rested her hand just inside the hole in the front wall of the annex closest to the target object with her arm outstretched (Fig. 4). She did not look at either the objects or the subject and at no point actively reached toward the target object. She did this for 10 s before the subject was let into the annex and then continued to hold the same position until the subject provided one of the objects. A fresh set of novel objects was also used.

Analysis

Coding and analyses were conducted in the same manner as in Experiment 1. Due to a camera error, videos from two trials could not be recovered. Inter-rater reliability was high (Cohen's $\kappa = 0.96$), and a third coder resolved all disagreements. In addition to using one sample t tests and binomial tests to compare subjects' behavior to chance, we also used a paired-samples t test to compare subjects' performance in Experiment 1 and Experiment 2. One subject never returned any of the objects, and so data from this individual were not included in any statistical tests, leaving a total of 54 trials available for analysis.

Results and discussion

Subjects provided the experimenter with an object on 87 % of all trials. Although the experimenter did not actively reach toward the target object, subjects still gave the target object more often than chance ($M = 69$ %, $t_6 = 4.48$,

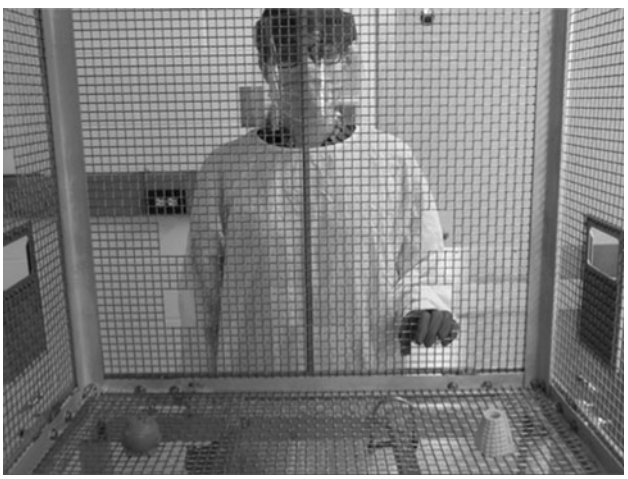

Fig. 4 Subjects' perspective upon entering the annex in Experiment 2. The target object is on the *right*

$p = 0.004$; Fig. 3). A binomial test confirmed this result ($p = 0.009$). Six subjects gave the target object more often than the distractor, and a single subject gave the two objects equally often. This pattern of performance provides evidence against a second attentional spotlighting account of capuchins' behavior in this task. Specifically, it suggests that the subjects did not give the target object more often because the movement around that object attracted them to it. In fact, subjects were not any more likely to first return the target object in Experiment 1 than in Experiment 2 ($t_6 = 0.45$, $p = 0.669$).

It might be somewhat surprising that the use of an impoverished reaching cue did not significantly reduce the rate at which subjects gave the target object in Experiment 2 compared to Experiment 1, in which a more explicit reaching gesture was used. As noted above, if subjects had failed to distinguish between the target and distractor objects, we could have reasonably interpreted this as evidence that capuchins rely on active reaching and appropriate head orientation and eye gaze to infer that others' actions are object-directed. Indeed, there is evidence that capuchins are sensitive to head orientation and eye gaze when begging for food from a human experimenter (Hattori et al. 2007, 2010). The fact that the removal of these cues did not significantly alter the rate at which subjects gave the target object might suggest that they can use these cues to make sense of other agents' behaviors, but do not necessarily require them if other salient gestural and postural cues are present. In this case, the use of a static reaching action, appropriate body orientation (that is, E3 was oriented toward the objects, perhaps signaling that she was attending to them), along with relevant contextual information (e.g., the objects were placed into the annex by another experimenter, and E3 only approached the annex after the objects were in place, etc.) may have been sufficient to trigger a representation of the experimenter's action as an object-directed.

It is also possible that our capuchin subjects were able to infer that the static reaching gesture was object-directed in Experiment 2 despite the limited cues available because Experiment 1 had familiarized them with the general features of the task. Warneken et al. (2007) reported that although in an initial study both human children and chimpanzees helped retrieve an out-of-reach object more often when an experimenter reached toward it than when he simply looked at it, in a second study neither the chimpanzees nor the children differentiated between a reaching and a non-reaching condition. The authors suggested that this might have been a carryover effect from the first study, and this explanation might be true for the capuchins in our study as well; however, these results also raise the possibility that mere hand proximity attracted subjects preferentially to the target object. This third attentional spotlighting account is addressed in Experiment 3.

Experiment 3

In this experiment, we tested whether capuchins would give an object that an experimenter's hand was closer to even when all other indicators that the experimenter wanted that object were removed. Specifically, the experimenter who had placed the objects into the annex now positioned her hand closer to one of the objects and then oriented away from the objects. We reasoned that if hand proximity alone attracted subjects to the target object, then they would still give the target more often than the alternative object despite the absence of any other goal- or object-directed cues. In contrast, if capuchins were relying on a more sophisticated set of behavioral cues when choosing between the two objects, then they might fail to differentiate between target and distractor objects in this case.

We chose to use this particular manipulation because there is evidence that many different primate species are sensitive to overall body and head orientation when interacting with other agents. When given the opportunity to steal a piece of food from a human competitor, chimpanzees (Hare et al. 2006), rhesus macaques (Flombaum and Santos 2005), and ring-tailed lemurs (Sandel et al. 2011) all preferred to steal food located behind the experimenter's back (rendering the experimenter unable to see the food) compared to food placed in front of the experimenter. These results are additionally supported by those obtained through the use of more cooperative tasks. Kaminski et al. (2004) found that a sample of chimpanzees, bonobos, and orangutans was more likely to beg for food from an experimenter when her body and face were oriented toward the subject than when her body and face were oriented away from the subject (see also Tempelmann et al. 2011). Similarly, Hattori et al. (2010) reported that capuchin monkeys directed more begging behaviors toward an experimenter whose body was oriented forward and eyes open than from one whose back was turned. Converging evidence also indicates that many species of primate are able to follow the direction of others' gaze as indicated by the orientation of their body and head (for a review, see Rosati and Hare 2009). In this way, overall body and head orientation seem to be postural features that primates attend to in a variety of contexts.

Methods

Subjects

Seven capuchins participated in this study. One capuchin (Auric Goldfinger) who had participated in the previous experiments was separated from the group at the time of testing and was consequently unable to participate.

Procedure

The procedure used in Experiment 1 was modified slightly. The front wall of the annex was altered so that in addition to the four holes embedded in the mesh, there were two additional (65 × 50 mm) holes through which subjects could return objects. These two holes were located just to the right and to the left of the horizontal midpoint of the front panel (visible in Fig. 5). After placing the two objects into the annex, rather than leaving the testing room, E2 gently rested her hand just inside the hole in the front wall of the annex closest to one of the object (the target) in the same manner as E3 had done in Experiment 2. However, critically, after placing her hand, E2 oriented away from the annex. After E2 had placed her hand in this manner, E3 walked over to the annex and held her hand out, palm up, directly between the two new holes in the front panel of the mesh (Fig. 5). She did not look at either object or at the subject. In this way, E3's hand was equidistance between the two objects in the annex, but E2's hand was closer to the target object. All other procedures remained unchanged with the exception that a new set of objects was used.

Analysis

Coding and analyses were conducted in the same manner as in the previous experiments. Inter-rater reliability was high (Cohen's $\kappa = 0.96$), and a third coder resolved all disagreements. One trial was removed from analyses due to an experimenter error, leaving a total of 55 trials for analysis.

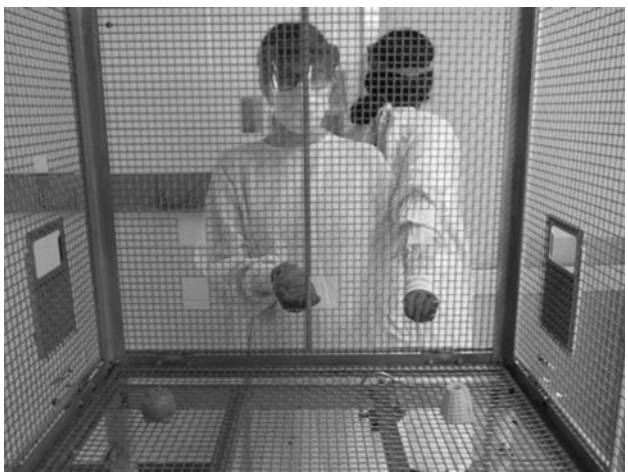

Fig. 5 Subjects' perspective upon entering the annex in Experiment 3. The target object is on the *right*. E2 is oriented away from the objects, and E3 is oriented toward the objects

Results and discussion

Subjects gave the experimenter an object on 100 % of trials. Unlike the previous experiments, subjects did not give the target object more often than the distractor object ($M = 51$ %, $t_6 = 0.27$, $p = 0.794$; Fig. 3). Binomial tests also confirmed that the number of times that subjects gave the target object was not significantly different from chance ($p = 1.000$). Two subjects gave the distractor object more often than the target, three gave the two objects equally often, and two gave the target object more often. These results indicate that capuchins did not simply select whichever object was closer to the experimenter's hand, but instead adopted an alternative strategy when choosing between the two objects. Such a strategy might involve attending to a number of different postural factors, including perhaps hand and arm position as well as general body and head orientation.

Note that although subjects' performance provides evidence against the attentional spotlighting account it was designed to address, we can only speculate as to precisely why subjects failed to show a preference for the target object. One hypothesis is that capuchins require both relevant gestural and postural information to interpret actions as object-directed. If this is the case, then the results of Experiment 2 might suggest that each of these cues can independently be relatively minimal. An outstretched (but not actively reaching) arm combined with appropriate body orientation (and not obviously incorrect face orientation) may be sufficient. Alternatively, when presented with conflicting gestural and postural cues, capuchins may prioritize postural cues, and consequently, subjects may have failed to interpret E2's outstretched arm as object-directed. Still another hypothesis is that subjects did interpret E2's action as object-directed, but failed to act in accordance with this. Subjects may have preferred to interact with E3 because she was oriented forward facing them and thus in a position to more easily receive an object and deliver a food reward. Each of these possibilities warrants further exploration in future studies.

Although the results of Experiments 1–3 seem to rule out several different attentional spotlighting accounts of capuchins' behavior in out-of-reach object tasks, they also raise the possibility that subjects chose between the two objects based not on which object the experimenter directed her reach toward, but instead based on which object was the easiest to give. According to this interpretation, when E3's hand was closer to the target object (as was the case in Experiments 1 and 2), it was slightly easier for subjects to give that object. In contrast, when E3's hand was equidistance between the two objects (as in Experiment 3), the two objects were equally easy to give to the experimenter and so subjects did not show a preference.

We hypothesized that this explanation was somewhat unlikely given that subjects did not generally seem to adopt a minimally effortful strategy in the task. For example, subjects would often handle both objects prior to giving one object to the experimenter. Nevertheless, this possibility was addressed directly in Experiment 4.

Experiment 4

In our final experiment, the experimenter actively reached toward and attempted to obtain the target object, much as she had done in Experiment 1. However, we made sure that it was no easier for subjects to give the target object to the experimenter than it was to give the distractor object. We reasoned that if subjects had given the target object more often in Experiments 1 and 2 only because it might have required slightly less effort to do so, then they would fail to give the target object more often when giving the target and distractor objects were equally effortful.

Methods

Subjects

All eight subjects participated in this study.

Procedures

To control for effort, we altered several features of the design from Experiment 1. First, we altered the front panel of the annex, so that there were now only two adjacent trading holes embedded in the mesh, one located just to the right and the other located just to the left of the horizontal midpoint of the panel (visible in Fig. 6). Second, after E2 placed each object into the annex through each hole in the left and right side panels of the annex, she used metal sliders to block these two holes (blocked holes visible in Fig. 6). These two changes were made to ensure that subjects could only give E3 an object through the two holes located in the center of the front panel. Third, after approaching the annex and looking at the two objects, E3 did not reach inside the annex through the hole closest to the target object to attempt to obtain it. Instead, she alternated between reaching underneath the floor of the annex, so that her hand was directly below the target object, and gently banging on the front panel of the annex in front of the target object as if trying to grab the target through the mesh caging of the annex wall (Fig. 6). While doing this, she held her other hand palm up directly between the two holes in the front panel. She did this for 10 s, after which the subject was allowed to enter the annex. Once the subject monkey entered the annex, the experimenter continued tracking and attempting to grasp the target object with her hand. Her other hand was always held centered between the two adjacent trading holes. Thus, it was never the case that upon entering the annex it was easier to trade the target object because the experimenter's hand was closer to that object. E3 alternated between looking at the target object and the subject monkey as she had done in Experiment 1. A different set of novel objects was also used.

Analysis

Coding and analyses were conducted in the same manner as in the previous experiments. Due to a camera error, videos from one trial could not be recovered. Inter-rater reliability was high (Cohen's $\kappa = 0.98$), and a third coder resolved all disagreements. Trials on which the subject did not return either object ($n = 1$) were not included in any statistical tests, leaving a total of 62 trials available for analysis. In addition to using one sample t tests and binomial tests to compare subjects' performance to chance, we also used a paired-samples t test to compare the percent of

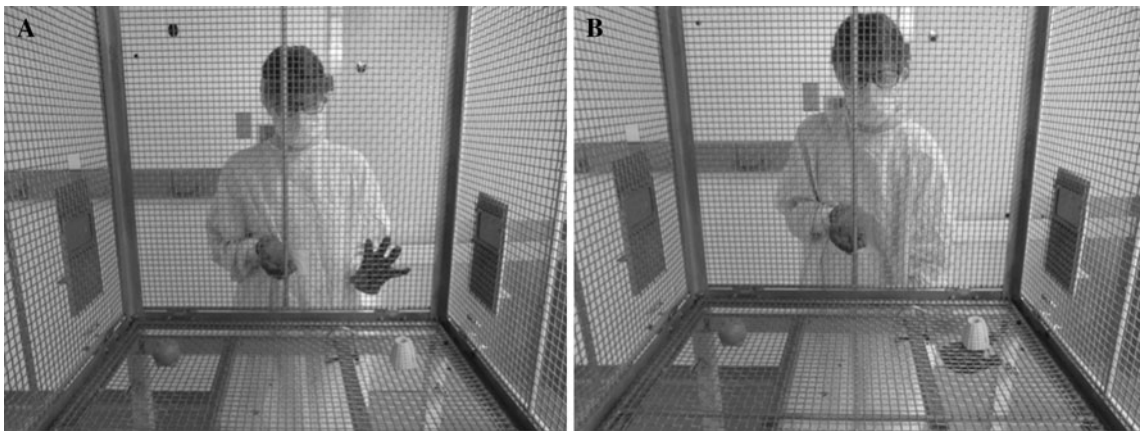

Fig. 6 Subjects' perspective upon entering the annex in Experiment 4. The target object is on the *right*. E3 alternated between positions **a** and **b**

trials on which subjects gave the target object in Experiment 4 to the percent of trials on which subjects gave the target object in Experiment 1. We chose to compare Experiments 1 and 4 because although an active reaching action was used in both of these experiments, only in Experiment 1 could a preference for the target object reflect subjects' use of a least effortful strategy.

Results and discussion

Subjects gave the experimenter an object on all but a single trial (98 % of the time). Once again, subjects provided the experimenter with the target object significantly more often than chance ($M = 70$ %, $t_7 = 3.85$, $p = 0.006$; Fig. 3). A binomial test confirmed this result ($p = 0.003$). At an individual level, six subjects gave the target object more often than the distractor object and two subjects gave the objects equally often. These results show that despite the fact that it was no easier to give the experimenter the target object as opposed to the distractor object, capuchins continued to do so preferentially. Furthermore, there were no significant differences in behavior between Experiments 1 and 4 ($t_7 = 1.00$, $p = 0.349$). These results suggest capuchins were not utilizing a minimally effortful strategy when choosing between the two objects. Additionally, these results address the possibility that subjects failed to give the target object more often in Experiment 3 because they were distracted by the presence of an additional human hand in the testing display. Note that in contrast to Experiments 1 and 2 (see Figs. 2, 4), in Experiment 3 (see Fig. 5) two hands are apparent in front of the mesh caging. However, two hands are also apparent in the testing display of Experiment 4 (see Fig. 6), and nevertheless, subjects gave the target object at levels greater than chance. Therefore, it seems unlikely that the mere presence of a second human hand caused subjects' failure to differentiate between the target and distractor objects in Experiment 3.

General discussion

Although the results of a number of different studies support the hypothesis that chimpanzees both represent others' goals in various helping contexts and are sensitive to these goals when actually helping others (e.g., Warneken and Tomasello 2006; Warneken et al. 2007; Yamamoto et al. 2009, 2012; Melis and Tomasello 2013), less work has addressed whether more distantly related species utilize goal representations when helping. The purpose of this series of experiments was to rule out the possibility that one helpful behavior that capuchins engage in, that is, giving a human experimenter an out-of-reach object, could be explained via one or more low-level attentional spotlighting accounts. In Experiment 1, we found that capuchins gave an experimenter an object that she was reaching toward more often than an ignored distractor object. This suggests that reaching did not simply make salient the option of giving *any* object in exchange for food. If this was the case, we would not have expected subjects to show a preference for the target object as they did in Experiment 1. The results of Experiment 2 indicate that capuchins did not provide the target object more often than the distractor simply because the experimenter's movement close to the target drew their attention to it. Even when a static reaching action was used, subjects continued to give the target object more often than chance. Experiment 3 showed that subjects did not always prefer to give the object to which an experimenter's hand was closer, indicating that subjects were not attracted to the target object solely because a human hand was nearer to it than to the distractor object. Finally, Experiment 4 confirmed that capuchins were not using a minimally effortful strategy in Experiments 1–3. Even when the desired target object was no easier to give than the distractor object, subjects continued to give the experimenter the target object more often than chance. These four experiments in combination demonstrate that capuchins' helping behavior in the out-of-reach object paradigm is not easily explained by several low-level explanations.

While the findings described here cannot be explained by the low-level attentional accounts we tested directly, our findings are still consistent with two alternative explanations: Capuchins may help based on an understanding of the experimenter's goal, or capuchins may instead simply be sensitive to the fact that other agents' actions are object-directed. Although the present experiments cannot differentiate between these two accounts, we think that a more mentalistic account of capuchins' behavior should be considered for several reasons. First, capuchins have demonstrated proficiency on a variety of different tasks in which another agent's mental state is relevant. Capuchins are sensitive to head orientation when begging for food from a human experimenter, which indicates that at minimum capuchins attend to the physical signs associated with attentional states (Hattori et al. 2007, 2010). Additionally, capuchins are able to use the emotional response of a conspecific to locate hidden food items (Morimoto and Fujita 2012). Perhaps most relevantly, capuchins seem to be sensitive to the intentions behind others' actions. In a study by Phillips et al. (2009), capuchins left a testing chamber earlier when a human experimenter acted as if she was unwilling to give them food compared to when she was unable to give them food either because of a physical obstruction or third-party interference. Furthermore, this pattern of behavior was only observed when an animate agent was involved.

Superficially, similar movements by inanimate rods did not elicit a similar pattern of responding, which the authors interpreted as evidence that capuchins attribute intentions to others.

For these reasons, although the experiments we presented here cannot distinguish between mentalistic and non-mentalistic accounts of capuchins' performance, we argue that it is possible that capuchins used goal representations to guide specific patterns of helping in our task. Of course, further evidence is decidedly needed to better evaluate this claim. One helpful future study could explore whether capuchins, like chimpanzees (see Yamamoto et al. 2012; Buttelmann et al. 2012), interpret similar behaviors differently depending upon the circumstances surrounding that behavior. Such a study might reveal important phylogenetic differences in constraints on helping. For example, we think it is likely that capuchins will be much more limited in the kinds of cues that they are able to use to infer others' goals and consequently will be very constrained in the range of helping behaviors they exhibit.

These series of experiments also raise the possibility that capuchins might be more motivated to help other individuals than previous studies have indicated (e.g., Barnes et al. 2008; Skerry et al. 2011). Note that if subjects had failed to give the experimenter the target object more often than the distractor object, we would not have known whether this failure was due to cognitive or motivational factors. Given that Barnes et al. (2008) found that capuchins helped at relatively low rates when no food was available, we might reasonably have predicted that capuchins would fail to give the experimenter the target object more often than chance but that this would be due to motivational rather than cognitive constraints. In reality, capuchins continued to preferentially give the experimenter the target object quite consistently in three out of four experiments even though they seemingly had no reason to do so. These results hint at the possibility that capuchins may not be entirely indifferent to others' goals. In other words, although food incentives seem to be necessary to elicit helpful behaviors in capuchins, subjects may preferentially choose to perform behaviors that *benefit others* over equivalently reinforced behaviors that provide no benefit. In this way, prosocial motivations may have played a role (albeit, a small one) in subjects' behavior on our task. Unfortunately, it is difficult to tease apart this account from one in which subjects were *solely* motivated by food. A subject who lacked prosocial motivations and was solely motivated by food rewards may still have shown the pattern of performance we observed in our task; such a subject may have spontaneously inferred that the goal object was the "right" object to give the experimenter in order to receive food. Our experiments cannot differentiate between these two accounts. In this way, from a motivational perspective, capuchins' performance may still be quite different from that of chimpanzees since chimpanzees are willing to help a human experimenter repeatedly even when they receive no food reward for doing so (Warneken et al. 2007).

The emerging body of work on helping behaviors in nonhuman primates will likely continue to highlight the extent to which humans' helping behaviors are exceptional. Even very young children exhibit impressive competencies in a variety of helping scenarios. Infants younger than 2 years of age will aid adults by pointing to the location of desired objects (Liszkowski et al. 2008), handing them out-of-reach objects (Warneken and Tomasello 2006; Warneken et al. 2007; Dunfield and Kuhlmeier 2010; Dunfield et al. 2011), and correctly solving a task that an adult has attempted to solve in an ineffective way (Warneken and Tomasello 2006). As children mature, instrumental helping becomes less dependent upon the presence of specific cues and actions that make salient a particular goal (e.g., verbal requests, pointing, reaching) and begins to be deployed with greater flexibility and sophistication. In contrast, instrumental helping in other primates is likely to be much more dependent upon cues that clearly indicate the need for help and that make salient the other agent's particular goal.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards This research was conducted in compliance with federal laws of the United States and with the regulations of Yale University. In addition, the studies reported here were reviewed and approved by the Yale University Institutional Animal Care and Use Committee.

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