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Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see?

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Capuchin monkeys were tested in five experiments in which two individuals competed over food. When given a choice between retrieving a piece of food that was visible or hidden from the dominant, subordinate animals preferred to retrieve hidden food. This preference is consistent with the hypotheses that either (1) the subordinate knew what the dominant could and could not see or (2) the subordinate was monitoring the behaviour of the dominant and avoiding the piece of food that it approached. To test between these alternatives, we released subordinates with a slight head start forcing them to make their choice (between a piece of food hidden or visible to the dominant) before the dominant entered the area. Unlike chimpanzees, *Pan troglodytes*, subordinates that were given a head start did not preferentially approach hidden pieces of food first. Therefore, our experiments provide little support for the hypothesis that capuchin monkeys are sensitive to what another individual does or does not see. We compare our results with those obtained with chimpanzees in the same paradigm and discuss the evolution of primate social cognition.

A number of experimental studies have addressed the question of whether nonhuman animals have an understanding of how the visual perception of others works and affects behaviour. In the hope of drawing inferences about human social cognitive evolution, the vast majority of these studies have focused on nonhuman primates (Tomasello & Call 1997; Povinelli 2000). For example, several experiments have examined whether apes understand that in order for another individual to see them the individual must maintain a certain posture (i.e. facing the subject with their eyes open and oriented towards the subject; Call & Tomasello 1994; Tomasello et al. 1994; Povinelli & Eddy 1996). Experimentalists have also investigated whether any primate species has the ability to assess what another individual can and cannot see (so-called Level 1 understanding of another's visual perspective; Flavell 1992).

It has been difficult to demonstrate something approaching Level 1 visual perspective taking in primates. For example, investigators have shown that a number of primate species follow the gaze of another individual, raising the possibility that primates understand that their groupmates see things that they do not (Povinelli & Eddy 1996; Emery et al. 1997; Tomasello et al. 1998). However, it is unclear whether gaze following represents a case of visual perspective taking (Povinelli & Eddy 1996; Tomasello et al. 1999, 2001). There have been other paradigms designed to explore the visual perspective-taking abilities of primates but studies that have produced positive results are potentially explained by simple learning hypotheses (Heyes 1993, 1998) while experiments producing negative results have been criticized for lacking ecological validity (Gomez 1996; Tomasello & Call 1997; Matheson et al. 1998; Shettleworth 1998; Hare 2001).

Recently, Hare et al. (2000) devised a new test to examine whether chimpanzees, *Pan troglodytes*, know what other chimpanzees do and do not see. Two individuals, one dominant to the other, were placed in rooms on opposite sides of a test room where food was positioned in different ways. They were then released into the test room to retrieve the food. For example, two pieces of food

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were placed between the subjects so that one subject could see both and the other could see only one of the food pieces (the food was hidden behind a small occluder). This paradigm was designed to help answer two questions: (1) are chimpanzees able to judge when another chimpanzee has visual access to food and (2) if they can assess when another individual cannot see food, can they use this information to develop a strategy for retrieving the food when competing against a conspecific? Initial results showed that subordinates preferentially retrieved food hidden from the dominant, while dominants preferentially retrieved food visible to the subordinate.

Although these results were consistent with visual perspective taking, it was possible that subjects were responding to behavioural cues given that the chimpanzees were released simultaneously. Therefore, in follow-up studies one subject was given a slight head start over the other. This delay forced subjects to decide which of the two pieces to approach before they saw where the competitor would go. The results were identical to the previous studies. Furthermore, several controls were run to rule out a number of competing hypotheses. From these results, Hare et al. (2000) concluded that chimpanzees know what conspecifics do and do not see and that they can use this information to formulate effective social strategies. These findings and conclusions have since been corroborated by other studies using similar competitive paradigms (Hare et al. 2001; Hirata & Matsuzawa 2001).

Although these results make it likely that our last common ape ancestor was able to assess what its conspecifics could see (at least in some situations) and benefit from this knowledge, further studies are needed to investigate the phylogenetic origins of this ability. For example, do the abilities of chimpanzees reflect general primate, or even mammalian, social cognitive abilities (i.e. potentially shared through common descent)? Alternatively, is the ability to assess what another individual can see a derived trait existing only within the hominoid clade?

The findings of a number of social cognitive studies in monkeys could be considered as consistent with the hypothesis that chimpanzees share the ability to assess what conspecifics can see with a number of monkey species (Byrne & Whiten 1990; Coussi-Korbel 1994; Hauser 1997; Fujita et al. 2002; Kuroshima et al. 2002). However, a number of studies are consistent with the hypothesis that monkeys do not understand how the visual perception of others works (Cheney & Seyfarth 1990; Povinelli et al. 1991; Kummer et al. 1996; Rendall et al. 2000).

In the light of previous research, our primary goal in this study was to address the current discrepancy in the literature on primate visual perspective taking. Although there is relatively little evidence to support the position that monkeys perform differently to apes in social cognitive tasks (Tomasello & Call 1997), Hare et al. (2000) suggested that chimpanzees can assess what conspecifics can and cannot see, while there remains little compelling evidence that monkeys also have this capacity. Is the discrepancy because monkeys, as with chimpanzees, are most likely to demonstrate their perspective-taking abilities when competing against conspecifics for food (Hauser 1997; Fujita et al. 2002), or is the difference between chimpanzees and monkeys real, and perhaps even an indication of different selective pressures on cognitive abilities?

To address these questions, we attempted a replication of Hare et al. (2000), using capuchin monkeys, a species whose cognitive abilities are commonly compared with those of chimpanzees (Visalberghi & McGrew 1997). Capuchin monkeys, as Platyrrhines, represent relatively distant relatives to the hominoids, with New World monkeys separating from Catarrhines ca. 40–45 million years ago (Klein 1999). Therefore, they are an excellent test species for investigating both (1) the origins of visual perspective taking in primates and (2) the utility of the Hare et al. (2000) method for further comparative studies. If capuchin monkeys know what conspecifics do and do not see while competing for food, it is possible this ability evolved as early as 40 million years ago before the New–Old World split and that this form of visual perspective taking is common among many monkey species throughout the primate order. In addition, if the Hare et al. (2000) competitive paradigm can be used with capuchin monkeys successfully, it is probable it can be used with a number of other primate and nonprimate species to test further evolutionary hypotheses.

EXPERIMENT 1

Experiment 1 was designed to assess whether (1) capuchin monkeys have a strict enough foraging hierarchy for our competitive test and (2) if capuchin monkeys readily compete over monopolizable food, are they strategic in their attempts to out compete competitors? We predicted that, as subordinates, capuchins would prefer to approach and retrieve hidden food that dominant competitors were unable to see. In addition, we predicted that the capuchins, as dominants, would switch strategies and try to monopolize the food by first taking at-risk, visible food pieces before collecting pieces that were safely hidden behind a barrier.

Methods

Subjects

Eleven adult and subadult capuchin monkeys (mean age 10 years) participated in this experiment and all subsequent experiments (the same number as in Hare et al. 2000 to provide equivalent statistical power). They were all born and reared in captivity and belong to two social groups at the Istituto di Psicologia. Capuchin monkey groups were housed in indoor–outdoor rooms (11–25 m^3) which were furnished with perches and slides; a variety of plastic toys and wooden blocks were given on a daily basis. All cages were connected by means of sliding doors. Monkey chow, fresh fruits and vegetables were given once a day in the early afternoon. Three times a week monkeys received a mixture of cheese curd, vitamins, egg, bran, oats and sugar as was their normal

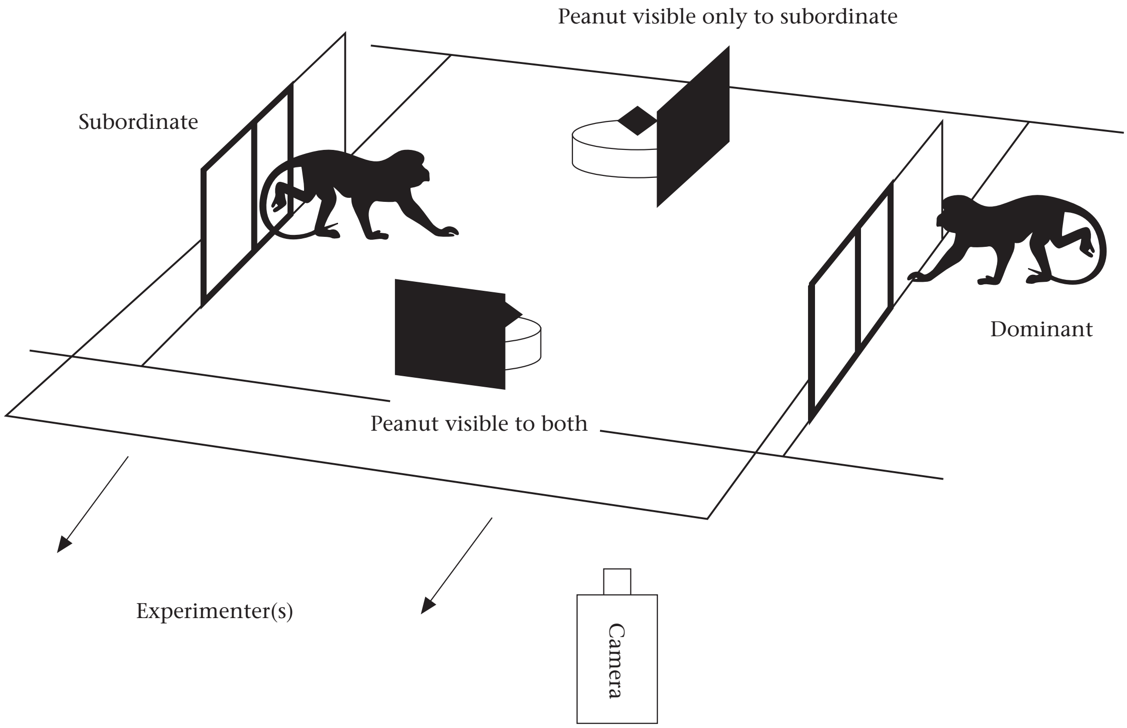

Figure 1. General experimental set-up in experiments 1–5.

routine. Water was available ad libitum and subjects were never deprived of food at any time. Nine of the capuchin monkeys were subordinate to someone else in their group while nine were dominant to someone else in their group (i.e. all individuals except the highest- and lowest-ranking individuals were both dominant and subordinate to other group members). When analysing the behaviour of the subordinates, we included only the nine subjects who were subordinate to someone in their group. Similarly, when analysing the behaviour of dominants, we included only the nine subjects who were dominant to someone in their group (this same procedure was used in all subsequent experiments as well).

Procedure

We tested subjects in a row of three indoor rooms each measuring 1.7 × 3 m and 2.6 m high, which were entered from a service hallway (see Fig. 1). The walls separating the rooms were concrete, as were the floors, while the ceilings and rear walls were wire mesh. Finally, the wall adjacent to the service hallway was glass so that experimenters could see and film the monkeys. The two outer cages each had sliding doors (50 × 50 cm and equidistant from each side of the walls) allowing animals to see either into the middle room when opened partially or to enter when opened fully.

Before testing began, we assessed each dyad in each of the two groups for dominance, using food competition tests. One subject was placed into each of the outer rooms and one piece of preferred food (a peanut) was placed on top of a small cylindrical platform (5 cm high and 12.4 cm in diameter) in the centre of the floor of the middle room (equidistant between the two subjects). The door of each subject was then opened slightly allowing each subject to see the food on the food platform and its competitor peaking through the other door. Then, both doors were opened simultaneously (the handles used to slide open the doors were connected so that experimenter 1 (E1) could open both doors simultaneously, see Fig. 1) and the animals were allowed to retrieve the piece of food. E1 scored which animal retrieved the food. We repeated this test four times for each dyad in a single session. In addition, in each session each dyad received a fifth trial in which an additional piece of food was placed on a second food platform. In this trial the two platforms were equidistant from both subjects (85 cm from each subject) and 80 cm from each other. Table 1 shows the results of the food dominance tests (which were further confirmed in the current experiment).

To ensure that the subjects had a chance to learn that food could be found on either hiding platform, we gave each subject three additional warm-up trials. In these trials both food platforms were placed just as in the last trial of the dominance testing, but the dominant was not released and only watched through the doorway (which was opened ca. 10 cm).

The test procedure was identical to the dominance testing except that two pieces of food were placed on food platforms equidistant between the two subjects (85 cm from each subject) with 80 cm between the platforms. In addition, a piece of opaque, black Plexiglas, 14.2 × 20 cm, was attached to each of the platforms. The pieces of Plexiglas made it possible to hide one or both pieces of food from one of the competitors because the platform (and Plexiglas) could be swivelled in place. Therefore, the platform could be turned so that the food placed on it was

Table 1. Age, sex, birthplace, experiment participation, rearing history and dominance rank of the subjects included in each of the experiments

Subject	Age (years)	Sex	Rearing history	Dominance rank
Group 1				
Pepe	13	Male	Human reared	1
Cognac	13	Male	Mother	2
Robot	5	Male	Mother	3
Paquita	10	Female	Human reared	4
Roberta	14	Female	Human reared	5
Robin H	3	Male	Mother	6
Robiola	2	Female	Mother	7
Group 2				
Gal	10	Male	Human reared	1
Rame	13	Female	Mother	2
Paprica	11	Female	Human reared	3
Carlotta	16	Female	Human reared	4

either occluded by the barrier or visible to both subjects (see Fig. 1).

Before each trial, the platforms were baited while one subject was waiting in each of the side cages. The sliding doors were closed so that neither subject could see the baiting. In each trial the middle room was baited in one of four ways.

(1) Visible–Visible. The food platforms were turned so the Plexiglas did not prevent either animal from seeing both pieces of food.

(2) Hidden–Hidden. Both of the food platforms were turned so that the subordinate could see both pieces of food while the dominant could see neither.

(3) Visible–Hidden. The food platforms were placed so that the subordinate could see both pieces of food but the dominant could only see one piece of food.

(4) Visible–Hidden (S). The food platforms were turned so that the dominant could see both pieces of food but the subordinate could see only one.

After baiting, E1 left the middle cage and partially opened the subjects' doors to allow both animals to look into the middle room at the food platforms and at their competitor. Once both competitors had looked through their respective doors, they were released to retrieve the food. Once both pieces of food were removed from the platforms, the trial was over. All trials were videotaped.

We tested all possible pairings of dominant–subordinate animals in both groups once in each condition. Therefore, there were 27 dyads (27 dyads were also used in Hare et al. 2000) which each received one session of four trials for a total of 108 trials. Across subjects, we counterbalanced the order of conditions.

In addition, after the testing was completed, we conducted a nonsocial control test to see whether any of the animals' preferences in the competitive experiment were produced by nonsocial factors such as a preference for food in front of barriers. Therefore, we gave five of the subjects four trials in which they were released individually into the middle cage where both food platforms were baited. In each trial, one platform was turned so that the occluder was behind the food while the other was turned so that the occluder was to the side of the food as in the Visible–Hidden test conditions). The two positions were both given twice on the right side and twice on the left for each subject.

Scoring and data analysis

In each trial, E1 recorded which subject(s) approached and who obtained which piece of food. A no approach was scored if an animal did not leave its cage before its competitor had retrieved both pieces of food. Determining who approached and retrieved the food was straightforward and unambiguous in every case (and this is true in all of the subsequent experiments as well), but as a precaution we randomly selected 20% of the Visible–Hidden and Visible–Hidden (S) trials and scored the subordinates' retrieval and approach behaviour again for reliability. Interobserver agreement on food retrieval and approach behaviour were both 100% with a Cohen's Kappa of 1.0.

We used the Visible–Hidden (S), Hidden–Hidden and Visible–Visible conditions to assess the preferences of subjects as subordinates and the Visible–Hidden and Visible–Visible conditions to assess their preferences as dominants. Each individual received only one score for a given condition regardless of how many trials it had had. To do this, we converted the scores of all individuals to 'percentage success' scores. For example, a subject might be paired with four different animals on four different trials in the same condition and obtain two pieces of food. In this case, for this condition the subject would receive a score of 50%. We used this procedure to generate one number for each subject in each role (dominant or subordinate) for each condition. A Friedman test was used to test for overall effects of condition and post hoc comparisons were conducted. Therefore, Bonferroni corrections were used to control for multiple comparisons between conditions.

Results

The amount of food subjects retrieved as subordinates differed significantly between conditions (29.3%

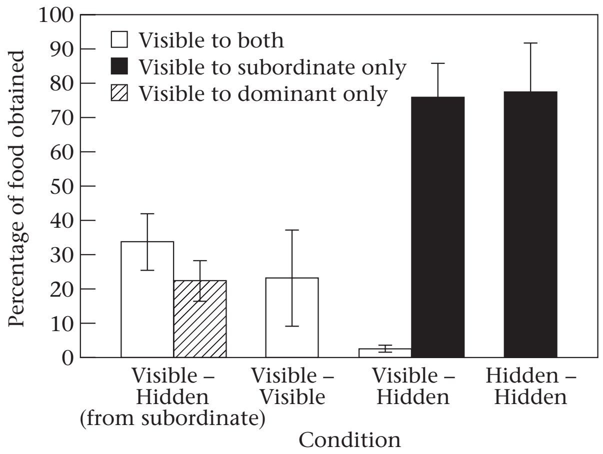

Figure 2. Mean percentage±SEM of pieces of food obtained by subordinates as a function of who had visible access to the food in experiment 1.

Visible–Hidden (S), 23.4% Visible–Visible, 34% Visible–Hidden, and 77.9% Hidden–Hidden; Friedman test: $\chi^2_2=15.65$, $N=9$, $P<0.001$; Fig. 2). Pairwise comparisons (all tests are one tailed unless otherwise specified) between conditions revealed that, as predicted, subjects retrieved more food in the Hidden–Hidden condition than in the Visible–Visible condition (Wilcoxon test: $T=45$, $N=9$, $P=0.004$; significance level 0.017, Bonferroni correction) or the Visible–Hidden conditions (Wilcoxon test: $T=45$, $N=9$, $P=0.004$). Although not significant, six subjects retrieved more food in the Visible–Hidden condition and one retrieved more food in the Visible–Visible condition (Wilcoxon test: $T=23$, $N=7$, NS).

The critical test is which piece of food subordinates preferred to retrieve within the Visible–Hidden condition (Fig. 2). As predicted, subordinates retrieved significantly more hidden food, taking 76.3%, while retrieving a mere 2.7% of the visible food ($T=36$, $N=8$, $P=0.006$).

Between conditions there was a significant difference in the approach behaviour of subordinates (Friedman test: $\chi^2_2=11.842$, $N=9$, $P=0.004$). Pairwise comparisons revealed that subordinates chose not to approach in 36.7% of trials in the Visible–Visible condition and in only 8.2% of trials in the Hidden–Hidden condition (Wilcoxon test: $T=15$, $N=5$, $P=0.023$).

In addition, we coded when subjects used unusual strategies while retrieving food. In seven trials involving three individuals, subjects waited to approach the food until the dominant entered and left the test area or were distracted eating a piece of food. Also in one trial a subject approached only after the dominant's back was turned.

Within the Visible–Hidden (S) condition no preference for retrieving visible or hidden food was detected for dominants (Wilcoxon test: $T=7$, $N=4$, NS). Most importantly, when dominants retrieved both pieces of food in the Visible–Hidden (S) condition they showed no preference for retrieving either the visible or hidden food first (Wilcoxon test: $T=15$, $N=6$, NS). Dominants' approach behaviour differed between conditions (Friedman test: $\chi^2_2=21$, $N=9$, $P<0.001$). Pairwise comparisons revealed that dominants chose not to approach significantly more in the Hidden–Hidden condition than in the Visible–Visible condition (Wilcoxon test: $T=28$, $N=7$, $P=0.009$).

Finally, when tested in the nonsocial control conditions, subjects did not have a preference for food placed in front of a barrier (paired sample t test: $t_4=1$, NS)

Discussion

The results of this first experiment make it clear that the competitive paradigm is a viable test for assessing the visual perspective-taking abilities of capuchin monkeys. First, even though capuchins are considered a tolerant species, the subjects demonstrated that they had a strict enough food dominance hierarchy for the competitive test to work. Second, these results look much like those of the chimpanzees, at least with respect to the subordinates. Between conditions, subordinates retrieved more food as the number of hidden pieces of food increased. In addition, subordinates retrieved more hidden than visible food within the Visible–Hidden condition. Finally, subordinates approached significantly less when both pieces of food were visible to the dominant than when they were hidden. In contrast, as dominants, the capuchin monkeys did not behave like the chimpanzees. Dominant capuchin monkeys did not preferentially retrieve the visible food first when both pieces were retrieved, even though, if one is trying to monopolize the food, it is best to take the at-risk visible piece first.

Overall, the performance of the capuchin monkeys, as subordinates, is consistent with the interpretation that they know what others do and do not see while, as dominants, their performance is not. None the less, several alternative explanations are viable in both cases. The most obvious explanation is that subordinates are simply reacting to the dominant's behaviour when deciding when to approach and which piece to retrieve. In favour of this interpretation is the fact that subordinates retrieved more food and approached more in the Hidden–Hidden condition, the one condition in which the dominants approached significantly less. The fact that the dominants did not show a preference for visible food might be because they were successful at getting food without the use of a strategy.

EXPERIMENT 2

In experiment 1, as subordinates, capuchin monkeys clearly showed a preference for the hidden food while as dominants they showed no preference. The purpose of experiment 2 was (1) to increase the potential for comparison between the performance of the capuchins and chimpanzees by ensuring the capuchin monkeys had as much experience competing (i.e. the same number of trials in each of the test conditions) as the chimpanzees had had before the critical delay test (experiments 3 and 4) and (2) to see whether subjects, as dominants, show more strategic behaviour in their food retrieval if the situation is made more competitive by moving the food closer to the subordinate. Our predictions were the same as for experiment 1.

Methods

The same 11 subjects from experiment 1 participated in this experiment (nine subjects played the role of subordinate and nine the role of dominant). The test procedure was identical to the previous experiment with three exceptions. (1) The Hidden–Hidden condition was dropped and replaced by an additional Visible–Hidden trial. Therefore, in each session a dyad received one trial of the Visible–Visible condition, one trial of Visible–Hidden (S), and two trials of Visible–Hidden for a total of four trials per session. (2) In the Visible–Hidden (S) condition the food platforms were both moved so that they were 45 cm from the subordinate and 125 cm from the dominant. (3) A new set of white, curved, plastic barriers (19.5 × 16 cm) were used as occluders.

Otherwise, as in experiment 1, E1 placed one monkey in each of the outer cages and closed the sliding doors completely. Then E1 baited the middle cage in one of three ways (instead of four as in experiment 1). Then, E1 partially opened both sliding doors to allow each animal to view the food platforms and see its competitor. After both animals had looked through their door, they were both released. E1 scored which animal(s) approached and who retrieved which piece of food.

We tested all possible pairings of dominant–subordinate animals in both groups in each condition once. As in experiment 1, there were 27 dyads and four trials per session for a total of 108 trials. Across subjects, the order of conditions was counterbalanced. Scoring and analysis were the same as in experiment 1. We randomly chose 20% of the Visible–Hidden and Visible–Hidden (S) trials and recoded the food retrieval and approach behaviour of subordinates for reliability. Interobserver agreement for food retrieval was 94% with a Cohen's kappa of 0.92 and for approach behaviour 97% with a Cohen's kappa of 0.87. Finally, as with the previous experiment, we conducted a nonsocial test after this experiment with each of the nine subordinates receiving four trials to test for any potential nonsocial factors that might explain any of the observed preferences in the competitive test. A Friedman test was used to test for overall effects of condition and post hoc comparisons were conducted. Therefore, Bonferroni corrections were used to control for multiple comparisons between conditions.

Results

The amount of food that subordinates retrieved between conditions bordered on significance (10.5% Visible–Visible, 24.2% Visible–Hidden, 27.6% Visible–Hidden (S); Friedman test: $\chi^2_2=5.79$, $N=9$, $P=0.055$; Fig. 3). Pairwise comparisons between conditions revealed that subordinates retrieved more food in the Visible–Hidden condition than in the Visible–Visible condition (Wilcoxon test: $T=33$, $N=7$, $P=0.017$; significance level 0.017, Bonferroni correction). Although subjects did not retrieve more food in the Visible–Hidden condition than in the Visible–Hidden (S) condition this is undoubtedly because in the Visible–Hidden (S) condition the food platforms were placed much closer to them than to the dominant. In addition, within the Visible–Hidden condition (Fig. 3) subordinates preferred to retrieve hidden food, taking 43.4%, while retrieving only 5% of the visible food (Wilcoxon test: $T=36$, $N=8$, $P=0.008$).

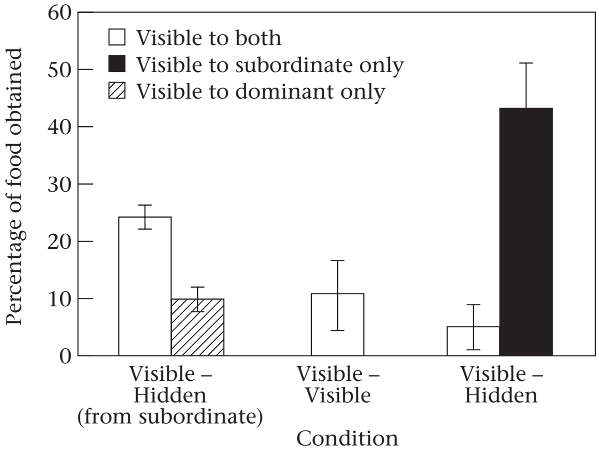

Figure 3. Mean percentage±SEM of pieces of food obtained by subordinates as a function of who had visible access to the food in experiment 2.

Subordinates chose not to approach in 54.7% of trials in the Visible–Visible condition when their competitor could see both pieces of food and refused to approach in only 30.5% of the Visible–Hidden condition when one piece was hidden from their competitor (Wilcoxon test: $T=34$, $N=8$, $P=0.012$). In addition, on two occasions (involving two individuals), subordinates waited until their competitor's back was turned before they attempted to retrieve food and on two occasions (involving two different individuals) subordinates took indirect routes when retrieving food.

For dominants, the most important comparison is within the Visible–Hidden (S) condition in which the food platforms were placed closer to the subordinate than the dominant. In this condition, dominants retrieved the more visible food (Wilcoxon test: $T=21$, $N=6$, $P=0.013$), but when they retrieved both pieces of food they showed no preference to retrieve the at-risk visible piece first (Wilcoxon test: $T=14$, $N=5$, $P=0.078$, two tailed). In addition, dominants approached the food in all conditions and in all but one trial, resulting in no difference between conditions (Friedman test: $\chi^2_2=2$, $N=9$, NS).

Finally, when tested nonsocially, subordinates showed no preference for food placed in front of a barrier nor did they exhibit a side bias; they did have a strong bias for the food platform in the rear of the test room (paired-sample t test: $t_8=4.619$, $P=0.002$).

Discussion

Experiment 2 corroborated the findings of experiment 1. Capuchin monkeys, as subordinates, preferentially retrieved hidden over visible food within and between conditions. In addition they approached less often when both pieces of food were visible to a dominant competitor than when one piece was hidden. One possible explanation for this approach behaviour is that when both pieces of food were visible, subordinates decided not to approach before they even saw the dominant approach. This interpretation is supported by the fact that the preference of subordinates for approaching more in the Visible–Hidden condition cannot be explained as a function of their interest in the food, given that more food was available in the Visible–Visible condition. In addition, this finding cannot result from decreased interest by dominants in the Visible–Hidden condition, because dominants approached in every trial but one across all conditions. It is possible, however, that when dominants see two pieces of food they are more excited or intimidating than when they see only one piece of food and the subordinates detect this before the trial or as the dominant approaches. Therefore, subordinates would preferentially approach when a piece of food is hidden. In addition, it is possible that once the dominants entered, taking the visible piece of food, they were less likely to move towards the second piece of food in the Visible–Hidden condition. Therefore, subjects would be more likely to approach in the Visible–Hidden condition. Either of these 'intimidation hypotheses' (Hare et al. 2000) would explain the observed difference. We designed experiments 3 and 4 to address these hypotheses.

Again in experiment 2, the dominants behaved as if they were using information about what their competitor could see. The critical finding is that when dominant subjects retrieved both pieces of food they did not first retrieve the at-risk visible piece. Dominants showed no preference, although the food in the Visible–Hidden (S) condition was placed much closer to the subordinate, making it more difficult for the dominant to retrieve both pieces of food. Therefore, as dominants, capuchins are either more tolerant of subordinates or are less strategic in their retrieval behaviour than chimpanzees. The former hypothesis seems implausible given that subordinates are clearly intimidated by the dominants approaching, often refusing even to approach (over half the trials in the Visible–Visible condition). Given that dominants showed little strategic retrieval behaviour, our further investigations focused solely on whether subordinates are taking the visual perspective of dominants. Finally, although in the nonsocial test subordinates showed a preference for the food platform in the rear of the test room, this preference apparently did not interfere with their food retrieval strategies.

EXPERIMENT 3

In completing the previous two experiments, the capuchins had similar experience to the chimpanzees before their delay test. Specifically, they received the same number of trials in each of the conditions, although the types of barriers and the order of the conditions were slightly different. Therefore, in experiment 3 we replicated the occluder experiment from Hare et al. (2000). This delay test is critical because it eliminates the possibility that the subordinate capuchin monkeys' preference for hidden food is due to their monitoring the dominant's approach behaviour. In experiment 3, we released the subordinate with a slight head start and noted which piece of food it first approached and which piece of food it retrieved. This allowed us to determine whether subordinates were using the dominant's behaviour when retrieving food or whether they based their decision on what the dominant was able to see. If subordinate capuchins know what others do and do not see they should approach and retrieve more hidden food. If subordinates react to the behaviour of their competitor they should approach randomly while preferring to retreive hidden food.

Methods

The subjects were the same 11 as in the first two experiments (nine played the role of subordinate). New occluders were used for this experiment, made of grey, opaque plastic (triangular in shape: 17.2 × 36 cm). The food platforms were baited in three different ways by E1.

(1) Visible–Visible. The food platforms were turned so that both pieces of food were visible to both animals.

(2) Hidden–Hidden. Both of the food platforms were turned so that the subordinate could see both pieces of food while the dominant could see neither.

(3) Visible–Hidden. The food platforms were placed so that the subordinate could see both pieces of food but the dominant could see only one piece of food.

After baiting, E1 partially opened the dominant's door while E2 partially opened the subordinate's door (the bar connecting the two door bars was removed allowing the two doors to be opened at different times) so that the animals could see the food platforms and each other. Once they were both looking through their respective doors the experimenters released the animals giving the subordinate a slight head start. E2 opened the door of the subordinate first. E1 then opened the door of the dominant as the subordinate approached a line drawn on the floor half way between its own door and the platforms. E1 then scored the initial direction of approach for the subordinate and which animal retrieved which piece of food. All trials were videotaped. If the subordinate chose not to approach for 30 s the trial was ended and a no approach was scored.

Each dyad received one trial of the Visible–Visible condition and the Hidden–Hidden condition while receiving four trials of the Visible–Hidden condition per session. We tested all possible pairings of dominant–subordinate animals in both groups. Therefore, there were 27 dyads and six trials per session for a total of 162 trials. Across subjects, the order of conditions was counterbalanced. Scoring and analysis were the same as in experiment 1. We randomly chose 20% of the Visible–Hidden trials and the food retrieval and approach behaviour of subordinates was coded by a second coder for reliability. This coder was blind to the location of the occluder when coding the direction of the subordinate's first approach. Interobserver agreement for food retrieval

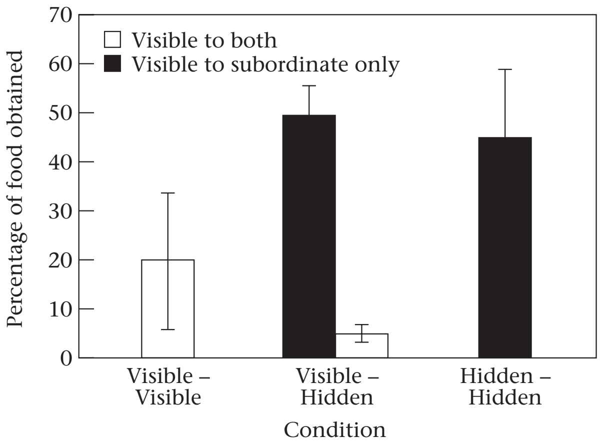

Figure 4. Mean percentage±SEM of pieces of food obtained by subordinates as a function of who had visible access to the food in experiment 3.

was 95.7% with a Cohen's kappa of 0.94 and for the direction of first approach 95.7% with a Cohen's kappa of 0.92. Finally, as with all the previous experiments, we conducted a nonsocial test after the experiment with each subordinate receiving four trials to test for any potential nonsocial factors that might account for the observed preferences in the competitive test. A Friedman test was used to test for overall effects of condition and post hoc comparisons were conducted. Therefore, Bonferroni corrections were used to control for multiple comparisons between conditions.

Results

Unlike previous experiments there was no difference in the amount of food that subordinates retrieved between conditions (30% Visible–Visible, 45% Visible–Hidden, 50% Hidden–Hidden; Friedman test: $\chi^2_2=0.56$, $N=9$, NS). Although there was no significant difference between conditions, within the Visible–Hidden condition (Fig. 4) the subordinates did retrieve more hidden food (Wilcoxon test: $T=43.4$, $N=9$, $P=0.007$).

Because the door of the dominant was not opened until the subordinate began to approach, subordinates approached in all but eight trials and there was no difference between conditions (Friedman test: $\chi^2_2=0.2$, $N=9$, NS). Therefore, the critical test in this delay experiment is the direction of first approach that the subordinates took before the dominant was released within the Visible–Hidden condition. Subordinates did not preferentially approach the hidden food (Wilcoxon test: $T=17.5$, $N=7$, NS). Finally, as in the previous experiments, the nonsocial control test revealed that subjects did not have a preference for food hidden behind barriers or a side bias, but they did prefer to retrieve food on the rear food platform first (paired-sample t test: $t_8=4.619$, $P=0.002$).

Discussion

The results of this experiment are very different from those of the previous two experiments. Much of this difference is probably attributable to the subordinates being released with a slight head start over the dominant. For subordinates, there was no difference in their food retrieval or approach behaviour between conditions. The critical test is within the Visible–Hidden condition. If subordinates retrieved and approached hidden food more often in the previous experiments because the dominant was unable to see it, they should approach hidden food first and retrieve more of it within this condition. Although subjects did retrieve more hidden food, they did not preferentially approach it. Therefore, we are unable to rule out the likelihood that subordinates are basing their retrieval decision on the behaviour of the dominant.

There are two additional reasons why subordinates might not have shown a preference to approach hidden food. (1) The nonsocial control tests between each experiment show that while subjects did not have a preference for food hidden behind barriers they did have a strong preference for food placed on the rear platform near the back wall of the test room. It is possible that this bias somehow interfered with their decision making. However, this seems unlikely given that subjects did have a preference for hidden food in experiment 2 while showing the same preference in the nonsocial test. (2) Because subjects retrieved about 50% of the food in each of the three conditions (on average a piece per trial), it is possible there was no motivation for strategic behaviour. In the next experiment we addressed both of these possibilities.

EXPERIMENT 4

In this experiment we shifted the location of the food platforms because (1) it is possible that subordinates' previous preferences for the rear food platform may have somehow interfered with their decision making and (2) it is possible that subordinates might become more strategic if it was more difficult for them to obtain food. Therefore, we shifted the food platforms towards the rear of the testing room and towards the dominant competitor to reduce their platform bias while decreasing the chance they will successfully retrieve food. Our predictions were the same as for experiment 3.

Methods

The 11 subjects (nine subjects played the role of subordinate), opaque occluders and procedure were identical to those in experiment 3. The food platforms were both shifted 8 cm towards the rear wall of the cage and 40 cm closer to the dominant's door. Therefore the food platforms were 45 cm from the dominant and 125 cm from the subordinate before the trial started (the two barriers were still 80 cm apart).

Each dyad, again, received one trial of the Visible–Visible condition and the Hidden–Hidden condition and four trials of the Visible–Hidden condition per session. All possible pairings of dominant–subordinate animals in both groups were tested once. Therefore, there were 27

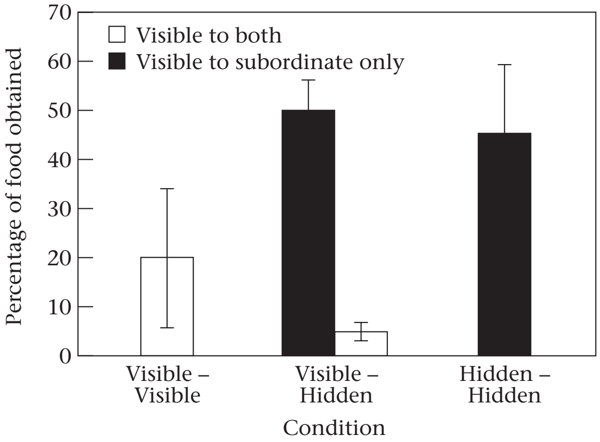

Figure 5. Mean percentage±SEM of pieces of food obtained by subordinates as a function of who had visible access to the food in experiment 4.

dyads and six trials per session for a total of 162 trials. Across subjects the order of conditions was counterbalanced. Scoring and analysis were the same as in experiment 1. We randomly chose 20% of the Visible–Hidden trials and the food retrieval and approach behaviour of subordinates was coded by a second coder for reliability. This coder was blind to the location of the occluder when coding the direction the subordinates first approached. Interobserver agreement for food retrieval was 95% with a Cohen's kappa of 0.93 and for the direction of first approach 95% with a Cohen's kappa of 0.91. Finally, as with all the previous experiments, we conducted a nonsocial test after this experiment with each subordinate receiving four trials to test for any potential nonsocial factors that might explain any of the observed preferences in the competitive test. A Friedman test was used to test for overall effects of condition and post hoc comparisons were conducted. Therefore, Bonferroni corrections were used to control for multiple comparisons between conditions.

Results

There was a difference between conditions in the amount of food that subordinates obtained (30% Visible–Visible, 45% Visible–Hidden, 50% Hidden–Hidden; Friedman test: χ^2_2=6.89, N=9, P=0.032; Fig. 5). Between conditions pairwise comparisons revealed that subordinates retrieved more food in the Hidden–Hidden condition than the Visible–Visible condition (Wilcoxon test: T=28, N=7, P=0.009). In addition, subjects retrieved more hidden than visible food (Fig. 5) within the Visible–Hidden condition (Wilcoxon test: T=27, N=7, P=0.014).

Although the subordinates' food retrieval changed from the previous experiment the approach behaviour did not. Subordinates refused to approach in only three trials making it impossible to test between conditions. The most critical result is which piece of food subordinates chose to approach first with their head start. Subjects did not preferentially approach the hidden piece of food first (Wilcoxon test: T=12.5, N=6, NS). As in the previous experiment, dominants approached in almost every trial and there was no difference between conditions (Friedman test: χ^2_2=3.85, N=9, NS). Finally, in the nonsocial control subjects did not prefer food in front of barriers, have a side bias or a bias for one of the food platforms over the other.

Discussion

The results of experiment 4 do not support the hypothesis that the subordinates are sensitive to what the dominant is able to see. Although subordinates retrieved more hidden food within and between conditions they did not prefer to approach the hidden food first when they were released with a slight head start over their dominant competitor. In addition, because the food platforms were shifted from their position in the previous experiments, this result cannot be a product of subjects' preference for one of the food platforms or the fact that the situation was not competitive enough. First, the subjects' previous preference for the rear platform disappeared in the nonsocial control test. Second, unlike the previous experiment, subordinates retrieved different amounts of food between conditions. Although these results do not support the possibility that subordinates assess what dominants can see, it is possible that there was simply too much social and nonsocial information to be encoded and processed before a social strategy could be implemented. The next experiment attempted to make the task simpler for the subordinates to test for this possibility.

EXPERIMENT 5

To reduce the burden of nonsocial information in this experiment, the capuchin monkeys only had to decide whether to approach and retrieve one piece of food. Sometimes this piece of food was visible to a dominant and sometimes it was hidden. If subordinates know what the dominant cannot see, they should approach and retrieve food more often or faster when it is hidden. If, while competing over food, subordinates rely on their competitor's behaviour, they should show no preference in their approach and retrieval behaviour between conditions.

Methods

The 11 subjects (nine subjects played the role of subordinate) and procedure were identical to that of experiments 3 and 4. The exceptions to this are that only one piece of food was hidden on the two food platforms in one of two ways and trials did not end after 30 s.

(1) Food Hidden. One platform was turned so that the subordinate could see the piece of food but the dominant could not. The second platform was turned so that both animals could see that it was empty.

(2) Food Visible. One platform was turned so that the subordinate could see that the platform was empty but the dominant could not. The second occluder was turned so that both animals could see the food.

As before, subordinate subjects were released with a head start. The dominant's door was not opened until the subordinate approached the line half way to the food. Unlike previous experiments, a trial did not end after 30 s. The experimenter waited until the subject approached and the food was gone before the trial was over. Each dyad received two trials of each condition per session and each of the 27 dyads were tested in one session for a total of 108 trials. E2 recorded who approached which food platform, and who retrieved the food. In addition, from the videotape the latency to approach was scored for the subordinate in each trial.

Results

Subjects retrieved almost equal numbers of food pieces between conditions, taking 38.7% of food in the Food Hidden condition and 40.3% in the Food Visible condition. In addition, the subordinates' mean latency to approach between conditions was identical (63.1 s in the Food Hidden condition and 63.3 s in the Food Visible condition). We also looked at the approach and food retrieval behaviour of subjects within the first 30 s (the length of a trial in experiments 1–4). In the first 30 s subjects retrieved 11% of the hidden food and only 2% of the visible food but this is not a significant difference (Wilcoxon test: $T=6$, $N=3$, NS). In addition, subjects chose not to approach in the first 30 s equally often between conditions (68.7% of Food Hidden trials and 68.7% of Food Visible trials).

Discussion

Even with less nonsocial information to deal with subjects still had no preference for retrieving or approaching the food hidden from the dominant. In addition, in the first 30 s of trials, there was no significant difference in the amount of food that subjects retrieved or approached between the two conditions. Therefore, it seems that reducing the amount of nonsocial information did not lead to more strategic behaviour. This negative finding was not due to the situation becoming less competitive given that only one piece of food was under contest. To the contrary, subjects within the first 30 s chose not to approach in almost 70% of trials and retrieved little food. It seems this experimental situation was competitive and there was a need for an effective social strategy.

GENERAL DISCUSSION

This series of experiments has demonstrated that when competing for food capuchin monkeys excel at reading the behaviour of conspecifics, but they do not use information about what others do and do not see. The competitive test worked well because, although capuchins are characterized as a socially tolerant species (Mendres & de Waal 2000), when competing over monopolizable food they show a clear foraging hierarchy. Every dyad within a group competed for food and the same individual consistently approached and retrieved more food than the other.

This initial result was confirmed by the first two experiments with subordinates consistently retrieving hidden food to avoid the dominant that was released simultaneously. In addition, the subordinates' preference for hidden food showed that they were at least sensitive to the behaviour of the dominant and possibly could judge to which piece of food their competitor had visual access. In experiment 2, the dominants also demonstrated sensitivity to the behaviour of others in retrieving more food visible to the subordinate. However, there is little evidence for visual perspective taking while playing the role of dominant, given that dominants did not prefer to retrieve at-risk visible pieces of food first when taking both pieces of food. Given the preference of subordinates for hidden food, the final three studies were designed to test the predictions of the visual perspective-taking and behaviour-reading hypotheses. In these delay studies the subordinate was released first only knowing that the dominant would soon approach, but did not see her behaviour when initially deciding which food piece to retrieve. If the subordinates' preferences in previous studies were a result of knowing what the dominant could and could not see, within the Visible–Hidden condition they should have continued to approach and retrieve hidden food even when they did not see the dominant approach. In contrast, if their preferences were a product of reading the behaviour of the dominant (i.e. to avoid the dominant), then subjects should have initially approached randomly, but with the entrance of the dominant avoid her by retrieving the hidden food.

In all three of these critical delay experiments without the approach behaviour of the dominants to rely upon, the subjects' approach and retrieval patterns were consistent with the predictions of the behaviour-reading hypothesis and not with the visual perspective-taking hypothesis. The subordinates' initial direction of approach within the Visible–Hidden condition in experiments 3 and 4 showed that they did not have a preference for approaching hidden food. At the same time, the subjects still retrieved more hidden food. Therefore, subordinates initially approached randomly, and then, upon the entrance of the dominant, adjusted their own approach (to avoid the dominant) and took the hidden piece of food. Finally, even in experiment 5, when the amount of nonsocial information was reduced, there was no evidence that subjects were taking into account what their competitor was able to see. Subordinates did not approach the hidden food quicker or more often than the visible food. Importantly, because less food was available in this experiment, the situation became more competitive. Within the first 30 s (the duration of trials in experiments 1–4) subordinates approached in fewer than half of trials and overall retrieved little food. Therefore, it seems there was a great need for an effective social strategy.

Although this competitive task was unable to demonstrate any evidence of visual perspective taking in capuchin monkeys, the capuchins were impressive in the way that they read the behaviour of their competitor and used strategies to avoid dominants and retrieve food, similar to that reported by Coussi-Korbel (1994) in mangabeys, *Cercocebus torquatus*. In fact, their behaviour-reading strategies were extremely effective in almost every context. Subordinates retrieved a large proportion of the food in almost every test.

Although our results show that capuchins perform differently to chimpanzees on this task, given that absence of evidence is not necessarily evidence of absence, it would be premature to conclude that capuchin monkeys have no ability for visual perspective taking. It is only after dozens of experiments and dozens of different approaches have been used that one can feel confident that null results might accurately reflect the ability of a test species (Heyes 1998). For example, future tests could be designed so that behaviour reading has little or no payoff in a similar competitive situation while assessing what others do and do not see has a high payoff. In this way, one would maximize the likelihood that the subjects might demonstrate any visual perspective-taking abilities they might possess. For example in the first four experiments, reading the competitor's behaviour may simply have been too effective to warrant assessing what another individual could see. In contrast in experiment 5, it is possible that dominants were simply too intimidating, keeping the subordinates from approaching at all. Perhaps designing an experiment similar to experiment 5 that limited the amount of nonsocial information needed while also reducing the competitiveness of the situation might yield more promising results. In addition, it might be fruitful to replicate and extend the paradigm developed by Fujita et al. (2002).

Although a negative finding from a single investigation does not typically allow for straightforward interpretations, we must emphasize that the original impetus of this experiment was to compare the visual perspective-taking abilities of capuchin monkeys with those of chimpanzees, using the same experimental methodology. For this purpose, the current experiments represent an adequate test. Like chimpanzees, capuchin monkeys have a clear foraging hierarchy, which allows the competitive food tests to be conducted. In addition, subordinates of both species showed that they were intimidated by the dominants in attempting to avoid them by retrieving more hidden food. Yet unlike chimpanzees, when capuchins did not have the approach behaviour of the dominants to use, they did not initially approach the hidden food.

In conclusion, capuchin monkeys perform differently from chimpanzees when competing for food. While subordinate capuchin monkeys are extremely sensitive to the behaviour of dominants, there was little evidence that they assess what conspecifics do and do not see when approaching and retrieving food. In contrast, Hare et al. (2000) found that chimpanzees were sensitive to the behaviour of their competitor, but also individuals changed retrieval strategies depending on the identity of their competitor and the visibility of the food. Further investigations will be needed with a number of species to test whether visual perspective-taking abilities predate the hominoid clade, but from this experiment there is no evidence that visual perspective-taking abilities evolved before the New World–Old World split 40–45 million years ago. Finally, it seems that the food competition paradigm will be a useful comparative tool in any future investigations into the evolution of perspective taking in many primate and nonhuman primate species (although this paradigm may not be suited for a species without clear foraging hierarchies such as the cottontop tamarin, *Saguinus oedipus*, K. Doherty, unpublished data).

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