Anim Cogn (2007) 10:439–448
DOI 10.1007/s10071-007-0088-1

ORIGINAL PAPER

Chimpanzees really know what others can see in a competitive situation

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Received: 31 March 2005 / Revised: 9 March 2007 / Accepted: 18 March 2007 / Published online: 11 April 2007

Abstract Chimpanzee's perspective-taking abilities are currently disputed. Here we show that in some food competition contexts, subordinate chimpanzees do take the visual perspective of dominant individuals, preferentially targeting a hidden piece of the food that the dominant cannot see over a piece that is visible to both individuals. However, the space where the animals compete is critical in determining whether subjects demonstrate this skill. We suggest that competition intensity, as mediated by these spatial factors, may play an important role in determining the strategy chimpanzees utilize in competitive contexts. Since some strategies may not require visual perspective taking in order to be successful, chimpanzees may not always demonstrate this skill. Differences in spatial arrangement may therefore account for the conflicting results of past studies.

Keywords Social cognition · Food competition · Visual perspective taking

Introduction

Several mammalian species follow the gaze direction of others to outside targets (Emery et al. 1997; Kaminski et al. 2004a; Miklosi et al. 1998; Tomasello et al. 1998). Chimpanzees and other apes even follow the gaze direction of others to hidden locations behind barriers, past distracters, and check back when they cannot find a target (Bräuer et al. 2005; Tomasello et al. 1999). Together, these findings suggest that Great Apes do not simply orient to targets that others are oriented to, but actually attempt to take the visual perspective of that individual. Sophisticated gaze-following abilities such as these may be adaptive, enabling individuals to obtain useful information about the location of food, predators, and group-mates. Indeed, knowing what conspecifics can see may be especially advantageous for individuals living in complex social groups. However, some researchers (Povinelli and Vonk 2003) have concluded that chimpanzees, as well as other nonhuman primates know very little about what others can and cannot see based on several alternative experimental paradigms in which chimpanzees seemingly fail to understand what others see.

In the first such paradigm, chimpanzees are confronted with two humans who have food placed between them (Povinelli and Eddy 1996). One of the humans has visual access to the chimpanzee, but the other does not; for example, one may be facing the chimpanzee, while the other has a bucket on her head. The chimpanzee must then choose to beg for food from one of these humans. They mostly chose randomly and did not prefer to beg from the human who could see them. The second type of paradigm where chimpanzees fail involves locating hidden food. Namely, chimpanzees are not very skilful at using the gaze direction of a human or a conspecific to locate food placed under one of two opaque containers (Call et al. 1998; Itakura et al. 1999; Bräuer et al. 2006). Even when chimpanzees can use such cues, they seem to use them as orientation rather than referential devices (Povinelli et al. 1997). Finally, chimpanzees fail a related hidden food task, failing to preferentially follow cues from a human who saw the location of the food reward, as compared to another human who was absent during the baiting process or who lacked visual access to it (Povinelli et al. 1990; Call and Tomasello 1999).

Hare et al. (2000) argued that chimpanzees fail these experimental paradigms not because they cannot take the

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visual perspective of others, but because the paradigms are all cooperative and/or communicative in nature. Although there is some evidence that chimpanzee cooperate in some contexts (Boesch 1994), it is nonetheless rare that one individual informs another about the location of a potentially monopolizable food resource (Hare 2001). Indeed, it is competition for (generally limited) food that characterizes the social life of chimpanzees and other primates (Sterck et al. 1997). Moreover, chimpanzees rarely face situations requiring that they choose which of two individuals to communicate with (neither of whom is directly looking at the subject). Indeed, even children had some difficulty with this task (Povinelli et al. 1997). These concerns with respect to the cooperative/communicative nature of previous experiments led Hare et al. (2000) to devise an experimental paradigm in which two chimpanzees spontaneously compete with one another over monopolizable food—without any training or intervention from humans. In a series of experiments, a dominant and a subordinate chimpanzee competed for two pieces of food, one of which could be seen by both of them and one of which could only be seen by the subordinate individual (because a barrier was blocking the dominant's visual access to it). The question was which piece of food the subordinate would pursue, and the prediction was that she would pursue the piece that the dominant could not see.

Results showed that subordinates did prefer to pursue the hidden food as predicted, suggesting that they were sensitive to what others can and cannot see. A series of control experiments ruled out several of the most obvious alternative explanations. (1) Subordinates did not simply prefer the hidden location, as without competition they went equally to the two locations. (2) Subordinates were not simply waiting and reacting to the dominant's behavior, as in some conditions they had a head start and had to choose first. (3) Subordinates did not perceive the barrier as a physical obstacle to the dominant, as they stayed away from food on their side of a transparent barrier (knowing that the dominant could see through it). (4) They were neither attracted to nor scared away from the hidden food based on the dominant's looking behavior under its door, since in some conditions subordinates had to choose while the door was still down.

Despite all of these control experiments, Karin-D'Arcy and Povinelli (2002) suggested that subordinates may simply prefer to forage next to barriers when a dominant individual is nearby (the peripheral feeding hypothesis). This hypothesis, however, is contradicted by an additional set of studies by Hare et al. (2001). In this study, the same group of chimpanzees was tested in a similar paradigm, but there were always two opaque barriers present—thus any preferences could not be due to the peripheral feeding hypothesis. The aim of that study was to test whether chimpanzees know what others had seen in the past, as opposed to what they could currently see, which was the focus of Hare et al. (2000). Subordinate chimpanzees always saw the whole baiting process, whereas dominants sometimes saw it and sometimes did not. Subordinates preferentially targeted the food if their dominant competitor had not seen the hiding process. Moreover, when one dominant saw the hiding process, but was quickly switched for another who did not see it, subordinates still pursued the hidden food. However, the authors found no evidence that subjects understood that the competitor may have different levels of knowledge about two different pieces of food. When the dominant was informed about one piece, but uninformed or misinformed about the second, subjects did not exhibit a preference. The authors suggested that the subjects may have had problems with this condition because they had to track two separate events (Hare et al. 2001).

Karin-D'Arcy and Povinelli (2002) failed to replicate the findings of Hare et al. (2000), concluding that the original results were unreliable, and that chimpanzees do not understand what others can see but rather use a variety of competitive strategies to succeed in such tests. Although subordinates did obtain more of the hidden food in this study, the critical reaching measure indicated that subjects did not prefer to reach for the hidden piece of food (as chimpanzees had done in Hare et al. studies). However, a difference in method may account for this discrepancy between the results of the two studies. In Hare et al. study, the size of the testing arena was 3.0×3.0 m^2 (9.0 m^2), but in Karin-D'Arcy and Povinelli (2002), the testing arena was 2.6×1.8 m^2 (4.68 m^2)—about half the size. Although the distance between subjects' door and food pieces were quite comparable in the two studies (1.5 m Hare et al. 2000 and 1.42 m Karin-D'Arcy and Povinelli 2002), the distance between the food pieces differed: 2 m in Hare et al. study and 1.25 m in Karin-D'Arcy and Povinelli study. These differences in space almost certainly changed the nature of the competition between chimpanzees—a fact noted in the follow-up study (Hare et al. 2001, p. 142). Even if the subordinate thought the dominant would approach the visible piece, the dominant would nonetheless get extremely close to the hidden piece because of the reduced distance between the two pieces. Moreover, this reduced distance might have also led the subordinate to predict that they could obtain both pieces before the dominant arrived: the arm length (including the hand) of an adult chimpanzee is ~76 cm for females and 78 cm for males (Bourne 1969), so this is a plausible assumption.

The main goal of the current study, therefore, was to determine whether chimpanzees really know what others can see in this type of competitive situation. Specifically, we wanted to investigate what factors would influence their behavior, hypothesizing that different spatial arrangements

would create different competitive regimes. Additionally, we attempted to replicate the main finding of Hare et al. (2000) using slightly different methods.

We used a new group of chimpanzees to ensure that visual-perspective-taking skills are not restricted to the subjects originally tested by Hare et al. (2000). Due to constraints on the testing cages, the space where the chimpanzees competed was smaller than in the original study. However, the distances between the two food pieces were similar (2 m). Following Karin-D'Arcy and Povinelli (2002), but in contrast to Hare et al. (2000), we used reaching for the food as the main measure of the chimpanzee's choice. We thought this was a better measure than approaching because it represents which piece of food the subordinate really wanted to choose. We also introduced conditions with one piece of food only, enabling comparisons across trials. Finally, we used buckets instead of barriers as occluders, and there was always two buckets present. The food was placed either behind the bucket (hidden food) or on top of the bucket (visible food). Two buckets were used to control for the peripheral feeding hypothesis.

Experiment 1

Methods

Subjects

Eleven adult and subadult chimpanzees (6–27 years old) participated in this study (see Table 1 for details). All subjects lived in a single group with 17 conspecifics in the Wolfgang Köhler Primate Center in the Leipzig Zoo (Germany). They were housed in enclosures with outdoor (4,000 m^2) and indoor areas (430 m^2), a resting cage (31 m^2), an observation room (25 m^2), and a set of five sleeping cages for the night (47 m^2). There were climbing structures, natural vegetation, and various enrichment devices such as puzzle boxes, logs, and ropes.

All subjects were captive born, but only the adult individuals were nursery-raised. They were fed four times a day on a diet of fruit, vegetables, and chow. Water was available ad libitum and subjects were not food deprived at any time.

Table 1 Subjects included in the study and role played in each experiment

Subject	Gender	Age (years)	Role played	
			Experiment 1	Experiment 2
Fraukje	Female	27	SUB and DOM	SUB and DOM
Corry	Female	27	DOM	DOM
Ulla	Female	26	SUB and DOM	SUB and DOM
Dorien	Female	23	SUB and DOM	DOM
Natascha	Female	23	DOM	DOM
Jahaga	Female	10	SUB and DOM	SUB and DOM
Gertruida	Female	10	SUB and DOM	SUB and DOM
Fifi	Female	10	SUB and DOM	SUB and DOM
Sandra	Female	10	SUB and DOM	SUB and DOM
Frodo	Male	10	SUB and DOM	SUB and DOM
Patrick	Male	6	SUB	SUB

SUB subordinate, *DOM* dominant

Materials

Testing took place in the sleeping cages. There were three adjacent cages: the cage for the dominant chimpanzee on the left, the cage for the subordinate subject on the right, and the testing cage in the middle. The mesh between the cages was blocked by black plastic panels for the experiment, making it impossible to see from one cage into the others. The middle cage was 2.5 × 2.6 m^2 (6.4 m^2)—in between the sizes of Karin-D'Arcy and Povinelli (2002) study and Hare et al. (2000) study—and 2.5 m high. The guillotine doors into the middle cage were in the middle of the left and right cages. The floor was bare, but there was one suspended platform on the back left corner where chimpanzees could rest. Subordinate subjects always entered from the right cage to control for the influence of that platform. We used two upside down buckets as barriers. They were placed on the extreme sides of the cage 1.65 m away from the door and 2 m from each other (as in Hare et al. 2000, study). Figure 1 shows the set-up during the test.

The two plastic buckets were 23 cm high and had a diameter of 28 cm on the bottom. On the top of each bucket was a plastic plate with a diameter of 30 cm, and another plate of the same size was half under the bucket, so that the noise would be the same when the experimenter placed the food visibly (e.g., on the plate on the top of the bucket) or hidden (behind the bucket from the dominant's view, on the plate on the floor). Pieces of banana were used for the food competition.

Procedure

We followed the basic procedure of Hare et al. (2000). Each subject was paired with a dominant individual, with dominance determined in a dominance test in the weeks before the test sessions began. This was the procedure for the dominance test: one animal was in the left cage, and one animal was in the right cage. In the first trial one piece of food was put in the center of the testing cage equidistant between the two connecting doors. Both guillotine doors were opened a bit from the bottom so that the two opponents

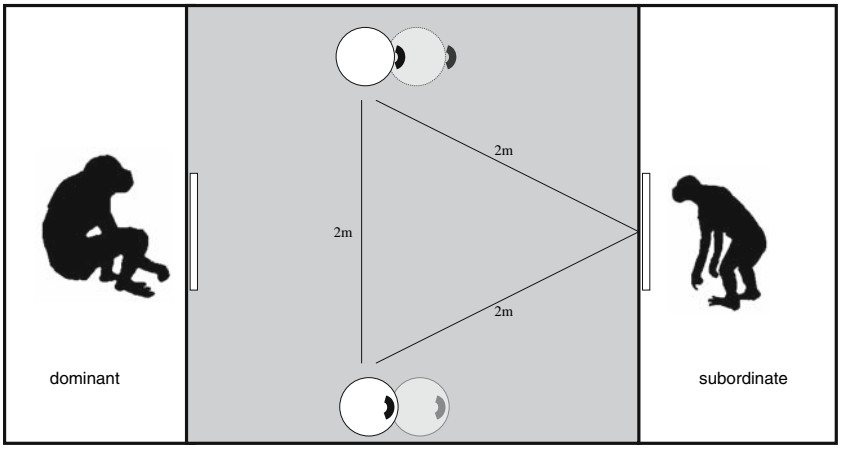

Fig. 1 Experimental set-up to scale in the condition Hidden–Visible for Experiment 1 (*gray buckets*) and Experiment 2 (*white buckets*)

could see each other and the food. The doors were closed again and then they were both opened at the same time so that the animals could enter the cage. In the second trial two pieces of food were placed on top of the two buckets that stood on the same places as in the testing situation. These two trials were presented again immediately before each experimental test session to make sure that the dominance did not change and to orient the subjects to the testing situation.

At the beginning of each experimental session the dominant individual was in the left cage and the subordinate was in the right cage with both doors slightly up so that the two opponents could see each other. After closing the doors the experimenter entered the testing cage to put the buckets in place (same for all trials) and the food in place according to condition. A test trial started when the door of the subordinate was opened a bit so that she could see the buckets and the food. Although subjects were encouraged to take a look by calling their names and moving the doors, a few of them (especially Ulla) only rarely looked through the gap. Then the door was closed again and immediately opened so that the subordinate could enter the cage. The door of the dominant animal was opened when the subordinate subject had entered the cage—which usually happened within 2 s. There were three experimental conditions, determined by how many pieces and where the food was placed.

Hidden–visible On piece of food was placed on the top of one bucket, a second piece was placed behind the second bucket. The dominant animal could see only one piece.

Hidden1 There was only one piece that was placed behind one bucket. The dominant could not see any food.

Visible1 There was only one piece that was placed on the top of one bucket, so that the dominant could see it.

Competitive pairs were created by pairing a dominant with a subordinate individual. In all cases, the subject of the experiment was the subordinate. Each pair of animals was tested in two trials in each condition, with order of trials randomized across subjects. So a daily session usually consisted of six experimental trials (and six related trials with noise that are not discussed in this paper) for a given pair. A subject was only paired with one dominant chimpanzee per day. If the dominant or the subordinate individual did not get any food in three trials in a row, we interspersed a filler-trial in which food was placed on top of each bucket. Animals were either released simultaneously, so that the dominant could get both pieces. Or only the subordinate was released, so that it got both pieces. This was to increase motivation to go for the food and to disrupt any potential biases on the part of the dominant (e.g., always shadow the subordinate).

Pairs were included in the analysis only if the dominance relationship was clear but the subordinate individual still sometimes went for the food. This means that for a pair to be included in the analyses: (1) the subordinate got both pieces of food in not more than one trial of the conditions with two pieces (e.g., Hidden–Visible); (2) the dominant got both pieces in all filler-trials when both were released simultaneously; and (3) the subordinate reached for a piece of food in at least one trial per session. Out of a possible 45 pairs, with nine animals playing the role of the subordinate subject (a 10th and a 11th was used as a dominant only), a total of 29 pairs were actually included in the analysis. As in Hare et al. (2000) and Karin-D'Arcy and Povinelli (2002), this meant that some subjects were tested in more pairs than others (from 1 to 7 pairs) because they had different numbers of opponents that were dominant to them. In the main analyses, each individual's score in a condition was the mean score from all pairs in which she participated. Because the exact dynamics of interaction is so important in this paradigm, especially in terms of dominance, we also conducted a secondary analysis in terms of pairs (but the results of these two approaches produced comparable results).

Scoring

The entire experiment was videotaped such that the subject and both buckets were visible. All trials were scored from the videotapes. For each trial we scored whether the subject (subordinate) entered the cage within 35 s, obtained the food and whether she reached for the food. All subjects entered the cages in all trials. We defined a reach as raising an arm in the direction of the food, before the dominant had approached any bucket. This movement of the arm was independent of locomotion. By definition a subject had to reach for the food if it took the food. For each subject we calculated the percentage of reaching for each type of food (hidden or visible) as the average for that subject across all pairs in which she played the subordinate role. We also had coded which bucket the dominant individual approached first.

An independent observer, blind to the hypotheses of the study, scored a randomly selected sample of 20% of the trials of the two experiments together. She coded (1) what bucket the subject would reach for, (2) what bucket the dominant would approach, and (3) whether the door of the dominant was opened at the correct time. Inter-observer-reliability was perfect for the reaching measure in Experiment 1 (Cohen's $\kappa = 1.00$, $N = 27$). As a check for whether the dominant used vision to find the food, we coded which bucket the dominant individual approached first. This was defined as getting close to the bucket within 10 cm. Again inter-observer-reliability was excellent in Experiment 1 (Cohen's $\kappa = 0.82$, $N = 27$). In order to check whether the door of the dominant was opened at the correct moment in the different conditions, the independent observer also coded for whether the cage door for the dominant individual was always opened immediately after the subordinate had entered the middle cage with the entire body. It was found that the door was opened too early in only 2 of 27 cases, no more than once in any experimental condition.

All statistical tests were one-tailed (unless otherwise indicated) since previous studies had shown that chimpanzees prefer to go for the hidden food in such a competitive situation. Due to the small sample size with used the exact Wilcoxon test.

Results

Subjects did not reach for a piece of food more often in the Hidden–Visible condition with two pieces than in the conditions with one piece (Hidden–Visible versus Hidden1 Wilcoxon $T = 24$, $N = 8$, $P = 0.461$, Hidden–Visible versus Visible1 Wilcoxon $T = 28$, $N = 8$, $P = 0.188$, both two-tailed).

Figure 2a shows the percentage of pieces that subordinates reached for in the Hidden1 and Visible1 conditions.

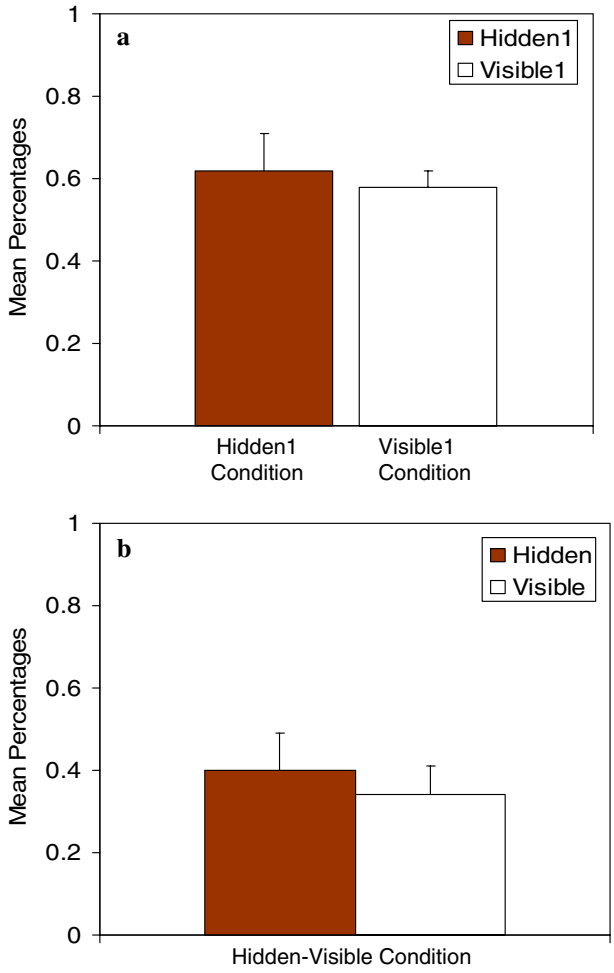

Fig. 2 **a** Mean percentage of food pieces (+SE) that subordinate chimpanzees reached for in the between-trial conditions (one piece available per condition) in Experiment 1. **b** Mean percentage of food pieces (+SE) that subordinate chimpanzees reached for in the Hidden–Visible condition in Experiment 1

There were no significant differences (Wilcoxon $T = 16$, $N = 7$, $P = 0.391$).

Figure 2b shows those conditions that afforded within-trial comparisons. In the Hidden–Visible condition subjects did not reach significantly more often for the hidden compared to the visible piece (Wilcoxon $T = 7$, $N = 4$, $P = 0.313$). Analyzing the performance on the level of the 29 pairs revealed similar results, that is, no reliable effects across conditions. (Hidden1 versus Visible1 Wilcoxon $T = 54.50$, $N = 13$, $P = 0.320$, within Hidden–Visible condition Wilcoxon $T = 39.50$, $N = 10$, $P = 0.142$).

We also analyzed whether learning effects over the course of the experiment. We compared the performance of the first half of trials to the second half of trials in each condition. We found no changes in the behavior of the subjects in any condition (Wilcoxon tests: $P > 0.05$ in all cases).

Dominants did not approach the bucket with the visible piece significantly more often than the bucket with the

hidden piece (Hidden1 versus Visible1 Wilcoxon $T = 30.5$, $N = 8$, $P = 0.086$, within Hidden–Visible condition Wilcoxon $T = 7$, $N = 4$, $P = 0.625$, both two-tailed). To assess the nature of the competition, we quantified the percentage of trials in which subordinates obtained food. Subordinates obtained a piece of food on average in 62% of the trials across conditions (Hidden1 = 55%, Visible1 = 50%, Hidden–Visible = 72%.

Discussion

Subordinate chimpanzees did not prefer to reach for the food that was hidden from the dominant, and thus in this experiment Hare et al. (2000) finding was not replicated. However, a problem in this study was that the subordinate subjects were very successful in obtaining food, regardless whether it was visible or hidden. On average, they obtained food in 62% of the trials across conditions. More importantly, they obtained the food in 50% of the trials in the Visible1 condition. This means that they were getting as much food as the dominant subjects when the food was visible. Subjects did not even behave differently in the conditions with one piece compared to the Hidden–Visible condition with two pieces—suggesting that they were comfortable with taking the visible food. Moreover, dominant individuals did not preferentially approach the visible piece. There are two possible explanations for this result. First, dominants may have not attended to the food, and simply approached any bucket. Alternatively, the dominants' approach may have been a reaction to the approach of the subordinate, since the dominant always entered last.

We hypothesized that the spatial arrangement in this experiment was the cause of these results. Specifically, the reduced competitive space may have led subordinates to use a different type of strategy: rather then pay attention to what the dominant did or did not see, the subordinates may have just tried to be fast and get as much food as possible. Note that the space in our testing cage (6.4 m^2) was smaller than in Hare et al. (2000) study (9.0 m^2). Similar problems arose in Hare et al. (2001) study, as well as in a study with capuchin moneys using the same paradigm (Hare et al. 2003). In those cases, the dominance relationship within a pair was not appropriate in the spatial arrangement, and subjects were probably comfortable with taking both pieces despite the presence of the dominant.

We therefore conducted a second experiment in which we explicitly manipulated the spatial arrangement of the testing arena, moving both pieces of food closer to the location of the dominant animal to increase competition between the two chimpanzees. That is, we modified the position of the food to make it more difficult for the subordinate to acquire food simply by being fast. We predicted that this spatial arrangement would make it more likely that the subordinate would use information about what the dominant was able to see.

Experiment 2

The purpose of the second experiment was thus to make the situation more competitive by moving both buckets and the food closer to the dominant's door. Consequently, speed should no longer be a viable strategy for subordinant individuals. As in the first study, if subjects knew what the dominant could perceive they should reach first for the hidden piece.

Methods

Subjects

We tested the same chimpanzees as in Experiment 1. One subject (Dorien) was not used as a subordinate in this experiment because her dominance relationships were no longer clear according to our criteria.

Materials

We used the same materials and set-up as in Experiment 1. The only difference was the location of the buckets, which were closer to the dominant to increase the competitive pressure on the subordinate. In the current Experiment the buckets were placed 2 m away from the subordinates' door and 1.3 m away from the dominants' door (still 2 m away from one another).

Procedure

The procedure was exactly the same as in Experiment 1. At the beginning of each session we tested the dominance again to make sure that the hierarchy did not change. We re-tested the hierarchy for the same pairs as in Experiment 1, but additionally we also tested some pairs that nearly passed our criteria to get into the analysis in Experiment 1. Using the same criteria for a clear dominance relation we got a total of 27 pairs with eight animals playing the role of the subordinate subject. Twenty-three pairs were the same as in Experiment 1, four pairs were new, and six pairs from Experiment 1 could not use anymore because the dominance relations had changed. Again some subjects were tested in more pairs than others (from 1 to 6 pairs) because they had different numbers of opponents that were dominant to them, and again in the main analysis and subjects mean values (within a condition across pairs) was the measure used (with analysis of dyads as a secondary analysis).

Scoring

We used the same dependent measures and analytical tools as in the previous experiment. As mentioned above, an independent observer, blind to the hypotheses of the study scored a randomly selected sample of 20% of all trials of the two experiments. Inter-observer-reliability was good in Experiment 2 for both the subordinate reaching (Cohen's $\kappa = 0.81$, $N = 40$) and the dominant's approach (Cohen's $\kappa = 0.96$, $N = 40$). No reliability was computed for the food acquisition measure because its outcome was totally obvious. In addition the independent observer coded whether the cage door for the dominant was always opened at the correct point of time. It was found that the door was opened too late in 1 of 40 cases.

Results

We calculated the percentages of trials in which subordinates obtained food to examine whether there was a higher degree of competition between the subordinate and dominant in this new spatial arrangement. Subordinates got a piece of food on average in 39% of the trials across conditions (Hidden1 = 39%, Visible1 = 24%, Hidden–Visible = 70%). This value represents a substantial reduction compared with the 62% found in the previous experiment. This indicates that obtaining food was indeed more difficult for subordinates. Moreover, in the Hidden–Visible condition with two pieces of food, they reached for a piece of food more often than in the conditions with one piece (Hidden–Visible versus Hidden1 Wilcoxon $T = 28$, $N = 7$, $P = 0.016$, Hidden–Visible versus Visible1 Wilcoxon $T = 36$, $N = 8$, $P = 0.008$, both two-tailed).

Figure 3a shows the percentage of pieces that subordinates reached for in the Hidden1 and Visible1 conditions. Subjects reached more often for the hidden compared to the visible piece (Wilcoxon $T = 15$, $N = 5$, $P = 0.031$).

Figure 3b shows those conditions that afforded within-trial comparisons. Subjects reached more often for the hidden food in the Hidden–Visible condition (Wilcoxon $T = 24.5$, $N = 7$, $P = 0.047$). Taken together, these results strongly suggest that the subordinates were indeed taking into account of what the dominant could and could not see.

Analyzing the performance on the level of the 27 pairs revealed similar results in the between condition comparison (Hidden1 versus Visible1 Wilcoxon $T = 99$, $N = 15$, $P = 0.012$) but not in the within condition comparison (Hidden–Visible Wilcoxon $T = 39$, $N = 10$, $P = 0.120$).

We also analyzed whether there were learning effects over the course of the experiment by comparing subjects' performance on the first trials to the last trials in each condition. We found no changes in the behavior of the subjects in any condition (Wilcoxon tests: $P > 0.05$ in all cases).

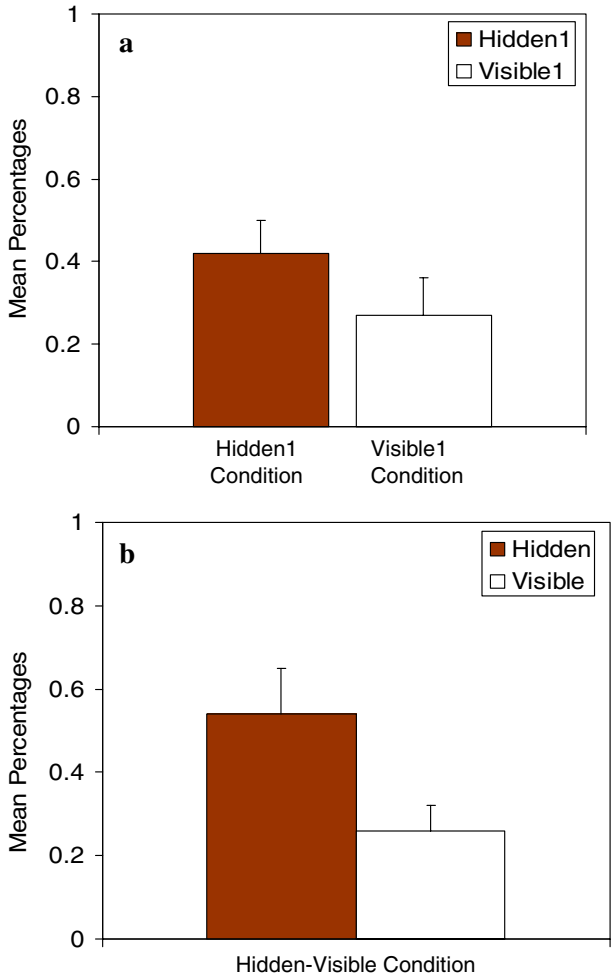

Fig. 3 **a** Mean percentage of food pieces (+SE) that subordinate chimpanzees reached for in the between-trial conditions (one piece available per condition) in Experiment 2. **b** Mean percentage of food pieces (+SE) that subordinate chimpanzees reached for in the Hidden–Visible condition (two pieces available per condition) in Experiment 2

Dominant chimpanzees approached the bucket with the visible piece significantly more often than the bucket with the hidden piece, comparing the Visible1 condition to the Hidden1 condition (Wilcoxon $T = 28$, $N = 7$, $P = 0.016$, two-tailed). Within the Hidden–Visible condition, however, there was no significant effect (Wilcoxon $T = 10$, $N = 4$, $P = 0.125$, two-tailed).

Discussion

Unlike the first experiment, subordinate chimpanzees clearly preferred to reach for the hidden food over the visible food. This was the case both for the within-trial and the between-trial comparisons. These results are similar in magnitude to those of Hare et al. (2000), even though in the current study, following Karin-D'Arcy and Povinelli (2002), we used reaching as the main measure instead of

approaching and/or obtaining the food. Importantly, the methods of our first and second experiments were identical except for the placement of the food. Subjects now obtained less food, and reached more often for the food when there were two pieces. Moreover, dominants preferentially approached the visible pieces (at least in the between-trial comparison), indicating that they did not simply shadow the behavior of the subordinates.

Since there were no significant learning effects within either study, it is likely that subordinates demonstrated visual-perspective-taking abilities in this experiment not because of a learned preference, but because repositioning of the food closer to the dominant created a more competitive situation.

General discussion

The current study had three main findings. First, in a more competitive situation (i.e., Experiment 2), chimpanzees know what their competitor can and cannot see. This replicates the main finding of Hare et al. (2000). Like that study, our second experiment had a number of features that served to rule out other potential explanations. For example, subordinates did not simply react to dominants' behavior, as subordinates always had a small head start and so had to choose first. Subordinates also were not reacting to the dominants' behavior, as the dominant's door was closed when the subordinate made her choice. By using the subordinate's first reach as a measure of preference, we ensured that we correctly scored the piece that the subordinate really chose to take. And finally, subjects did not learn to use this strategy during the course of either of the two experiments (they also showed no evidence of learning in either Hare et al. 2000, or Karin-D'Arcy and Povinelli 2002). Whatever skills they displayed, they brought with them to the experiments.

Although we believe that this experimental paradigm provides the most convincing evidence of chimpanzees' skills of visual perspective taking, it is important to emphasize that this finding is not discrepant with others in the literature. For example, this finding is consistent with the evidence from studies of primate gaze following that were mentioned previously. Gaze following skill, moreover, is not an inflexible response to a stimulus: from a certain age chimpanzees look where another individual is looking and, if they find nothing interesting on that line of sight, check back a second time and try again (Bräuer et al. 2005; Call et al. 1998). Indeed, if a chimpanzee follows another's line of sight and repeatedly finds nothing there, they will quit following that individual's gaze altogether (Tomasello et al. 2001). Another finding that is consistent with the current results is that when chimpanzees compete with a human over food, they show a strong preference for food that the human was not looking at; on some occasions thy may even attempt to conceal their approach to that food from the humans' view (Melis et al. 2006). All of this evidence converges on the same conclusion: chimpanzees know what others can and cannot see.

The second main finding of our experiment is that in competitive experimental paradigms such as this, the *intensity* of competition, and not the mere presence of competition, is crucial. Competition intensity may depend on many factors, including the subordinate's assessment of the speed of the dominant, the time lag in the release of the contestants, the dominant's level of excitement and attentiveness, and the precise dominance relation between the individuals (see also Karin-D'Arcy and Povinelli 2002). We found that an additional factor that may alter competition intensity is the spatial arrangement of the competitive arena. Thus, in our first experiment subordinate chimpanzees obtained food on well over half the trials, and so it is likely that they simply adopted a strategy of speed, attempting to acquire as much food as possible, rather than attending to what food the dominant could and could not see. In the second experiment, however, we increased competition intensity by placing the food closer to the dominant's door. Here, it was more difficult overall for subordinates to acquire food, and they paid attention to the dominant's visual perspective, preferring to target the food that the dominant could not see. Consequently, we believe the reason that Karin-D'Arcy and Povinelli (2002) did not replicate the findings of Hare et al. (2000) is simply that their space was too small to engender the kind of competition that would encourage the chimpanzees to use their perspective taking skill. The smaller space used in Karin-D'Arcy and Povinelli (2002) could have two effects on competition intensity. First, subjects may have refused to enter the cage and reach for the food at all, because to do so they had to move very close to the dominant. Proximity to the dominant may have made it difficult to escape in the event that the dominant charged. Second, subjects could sometimes monopolize both food pieces because they were close together. In fact, inter-food-distance predicts how easy it is to monopolize food (Mathy and Isbell 2001). If both pieces of food are monopolizable, visual-perspective-taking is not necessary to acquire food—and it may even be a good strategy to target the visible piece first (see also Hare et al. 2000, p. 11). Karin-D'Arcy and Povinelli (2002) reported both effects: subordinates often refrained from entering the cage, and obtained both food pieces in 25% of the trials in the Hidden–Visible condition.

There may be other reasons why the chimpanzees in Karin-D'Arcy and Povinelli's study (2002) failed to demonstrate visual-perspective taking. To begin with, that study had less statistical power then either the current study or the

studies by Hare and colleagues (2000, 2001). Whereas we had 29 and 27 chimpanzee pairs available for analysis, Karin D'Arcy and Povinelli had only 19 pairs. Their results were in the same direction as ours, but did not reach statistical significance. Second, Karin-D'Arcy and Povinelli analyzed only the trials when subjects exhibited a discrete first reach or first touch to a piece of food and obtained only one piece. This criteria may have ruled out important data. Another difference is that here we opened the door of the dominant as soon as the subordinate entered the cage, whereas Karin-D'Arcy and Povinelli waited until subjects reached for the food before opening the dominant's door. Moreover, they also encouraged their subjects verbally when they did not enter the cage; this might have influenced the subjects' behavior since humans also represent a type of dominant individual. Finally, the social structure in that group of chimpanzees may have differed from ours in important ways. For example, dominance hierarchy can vary among chimpanzee societies (Wittig and Boesch 2003). Since dominance structure and therefore the relationship between the pairs is crucial in this kind of experiment, it is possible that the chimpanzees in the current study (the group at the Köhler Primate Center) and in Hare et al. study (the group at the Yerkes Primate Center) had different dominance relations relative to the chimpanzees in Karin-D'Arcy and Povinelli (2002).

Competition for food plays an important role in the lives of social living primates such as chimpanzees. The socio-ecological model predicts that, other than predation risk, food distribution and therefore food competition is the key factor determining dominance relationship. Contest competition, where some individuals can exclude others from obtaining food, especially facilitates a clear dominance relationship (Wittig and Boesch 2003). Understanding what others can see may be a highly adaptive skill for such competitive animals, perhaps especially for subordinates as a way to gain access to food that is within the reach of a dominant but not visible to her. The advantage of the current experimental paradigm is that it used a relatively natural food competition situation between conspecifics, rather than a cooperative situation in which a human informed and/or actively shared food with a chimpanzee. This does not mean, of course, that knowing what others can see is not useful in a communicative situation as well. Indeed, chimpanzees adapt their gestures to the attentional state of the receiver of the signal (Hostetter et al. 2001; Kaminski et al. 2004b; Liebal et al. 2004). However, cooperative or communicative situations simply may not be appropriate when chimpanzees are required to make decisions specifically about food. Finally, the socio-ecological model, although developed around primate societies, suggests that other nonprimate species living in complex social environments may possess similar social cognitive skills (Rowell 1999). As such, one avenue of future research might be to test other social species—especially those for whom contest competition is the rule—in this same experimental paradigm.

In summary, we replicated the findings of Hare et al. (2000) with a new group of chimpanzees. Subordinates preferentially targeted the hidden pieces that the dominants could not see. We also found that the space where the animals competed was critical in determining the appropriate level of competition to reveal positive results. We suspect that the main reason why Karin-D'Arcy and Povinelli (2002) did not find this result was because their spatial arrangement was inadequate to encourage the use of perspective taking skills.

Acknowledgments We thank Julia Riedel, Hagen Lehmann, and Katrin Schumann for helping with data collection, and Tanja Lindner and Josefine Kalbitz for coding. We also thank Nora Tippmann for the drawings. Finally, we are very grateful to Alexandra Rosati for checking the style of the paper.

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