



Do chimpanzees know what conspecifics know?

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(Received 7 March 2000; initial acceptance 16 April 2000;

final acceptance 16 June 2000; MS. number: 6515)

We conducted three experiments on social problem solving by chimpanzees, *Pan troglodytes*. In each experiment a subordinate and a dominant individual competed for food, which was placed in various ways on the subordinate's side of two opaque barriers. In some conditions dominants had not seen the food hidden, or food they had seen hidden was moved elsewhere when they were not watching (whereas in control conditions they saw the food being hidden or moved). At the same time, subordinates always saw the entire baiting procedure and could monitor the visual access of their dominant competitor as well. If subordinates were sensitive to what dominants did or did not see during baiting, they should have preferentially approached and retrieved the food that dominants had not seen hidden or moved. This is what they did in experiment 1 when dominants were either uninformed or misinformed about the food's location. In experiment 2 subordinates recognized, and adjusted their behaviour accordingly, when the dominant individual who witnessed the hiding was replaced with another dominant individual who had not witnessed it, thus demonstrating their ability to keep track of precisely who has witnessed what. In experiment 3 subordinates did not choose consistently between two pieces of hidden food, one of which dominants had seen hidden and one of which they had not seen hidden. However, their failure in this experiment was likely to be due to the changed nature of the competition under these circumstances and not to a failure of social-cognitive skills. These findings suggest that at least in some situations (i.e. competition with conspecifics) chimpanzees know what conspecifics have and have not seen (do and do not know), and that they use this information to devise effective social-cognitive strategies.

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A recurrent theme in the study of primate cognition is the discrepancy between the cognitive skills that individuals seem to display in more natural settings and those that can be rigorously demonstrated in more controlled experimental settings. A case in point is the skills of chimpanzees, *Pan troglodytes*, in understanding what conspecifics do and do not see. Some researchers have reported anecdotes and other naturalistic observations of chimpanzees that seemingly demonstrate this ability (see Byrne & Whiten 1992). For example, Goodall (1971) reported that an individual who had spied fruit in a tree actively refrained from retrieving it, or even looking at it, when others were present (retrieving it only after the others had left the area). de Waal (1982) reported that chimpanzees sometimes actively hide parts of their body with their hands (e.g. fear grimaces), presumably so that

groupmates will not be able to see signals of their emotional state (see also Tanner & Byrne 1993, for a similar behaviour in gorillas, *Gorilla gorilla*). In other, more systematic studies, chimpanzees visually followed the gaze direction of both conspecifics and humans even around barriers and past distracters (e.g. Povinelli & Eddy 1997; Tomasello et al. 1998, 1999).

In two experimental paradigms, however, chimpanzees have seemingly failed to show an understanding of what others can and cannot see. First, chimpanzees given the choice of begging from a human who can see them versus one who cannot chose indiscriminately in all but the simplest conditions (Povinelli & Eddy 1996a; Reaux et al. 1999). That is, although they chose appropriately when one human was facing them and the other had her back turned, they chose indiscriminately when one human's view was occluded but the other's was not (e.g. when one human had a bucket over his head and the other did not). Second, when chimpanzees were given the task of finding food hidden somewhere in a row of opaque containers most individuals did not use human gaze as a cue for finding it, although some did (e.g. Povinelli & Eddy

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1996b; Tomasello et al. 1997; Call et al. 1998; Itakura & Tanaka 1998). Together, these studies suggest that the skills shown by chimpanzees in more naturalistic settings may not reflect a rich social-cognitive understanding of the visual experience of others, but rather some simpler skills involving the learning of social cues.

There may be a number of reasons for this inconsistent performance, however. One hypothesis is that these paradigms are unnatural, because in both of them a human communicates to a chimpanzee about a monopolizable food item. This situation is clearly unusual for chimpanzees who compete almost exclusively with groupmates for monopolizable food resources (Wrangham 1980; Hauser & Wrangham 1987). Thus, chimpanzees may not understand the cooperative motive of the human communicator in these experiments because it is dissonant with both the selective pressures their species has faced during its evolutionary history and with their own previous food-related experience.

Hare et al. (2000), therefore, designed a new experimental paradigm to test what chimpanzees know about what conspecifics can and cannot see, emphasizing competition between conspecifics rather than cooperation and communication with humans. In each of five experiments a subordinate and a dominant individual were placed in rooms on opposite sides of a middle room. Each of the extreme rooms had a guillotine door leading into the middle room. When these doors were partly raised at the bottom individuals could observe a human placing two pieces of food at various locations within that room, and to see the other individual looking under her door. After the food had been placed, the doors for both individuals were opened wide and they were allowed to enter the middle room. The basic problem for the subordinate was that the dominant took all of the food it could see, and indeed in all the experiments in which dominants had good visual and physical access to the two pieces of food they usually took both. However, in some cases the subordinate could see a piece of food that the dominant could not see, for example, it was placed on the subordinate's side of a small barrier. The question in these cases was thus whether the subordinates knew that the dominant could not see a particular piece of food, and so it was safe for them to go for it. This procedure is noteworthy relative to other experimental paradigms in that: (1) the chimpanzees interacted with conspecifics, not humans; (2) no training was involved; and (3) it involved competition, not cooperation, for food, which is arguably a more natural situation for nonhuman primates.

The main finding was that subordinates did indeed go for the food that only they could see much more often than for the food that both they and the dominant could see. A number of control conditions effectively ruled out the possibility that subordinates were monitoring the behaviour of the dominant or that they were responding to other aspects of the experimental situation. Of special importance: (1) the subordinate was given a small head-start so that it could not wait and react to the dominant's choice; and (2) on some trials the dominant's door was closed, so the subordinate could not even monitor the

dominant's behaviour behind the partially open door. The findings of this study thus suggest that chimpanzees do indeed know what conspecifics can and cannot see, and that they use this knowledge in food competition situations. The overall methodological point is that when a more naturalistic experimental paradigm was used, chimpanzees showed much more sophisticated social-cognitive skills.

This procedure may be used to test chimpanzees' understanding of psychological states that are more complex than visual perception. Most importantly, mainly negative findings have resulted from experimental approaches to what chimpanzees know about what others 'know'. Thus, Povinelli et al. (1990) found that chimpanzees preferred to ask for food from a person who had witnessed its hiding over someone who had not witnessed its hiding, the inference being that they could discriminate a 'knowledgeable' from an 'ignorant' human. The problem is that the apes in this study only learned to do this over many scores of trials with feedback on their accuracy after every trial (see Heyes 1993; Povinelli 1994, for details). Moreover, Povinelli et al. (1994) failed to replicate these results with another group of chimpanzees; Call et al. (2000) failed to replicate them with a procedure designed to make the task easier for subjects; and Call & Tomasello (1999) also found negative results in a related but slightly different procedure.

We therefore attempted to address the question of what chimpanzees know about what others 'know' (which in our experiments reduced to what chimpanzees know about what others have and have not seen in the immediate past) using the basic methodology of the Hare et al. (2000) food competition paradigm. In the first experiment, a subordinate saw one piece of food being placed on its side of one of two occluders, immediately before she had to compete for that food with a dominant. In one condition the dominant was allowed to witness the baiting (the informed condition), but since the food was always on the subordinate's side of the occluder, if she was to compete successfully she needed to recall where the food had been placed. In another condition the dominant was not allowed to see the food hidden, and so was uninformed of its location. In a third condition the dominant was misinformed about the location of the hidden food, that is, after she saw it hidden in one location it was then moved (when she was not observing but the subordinate was) to another location. The subordinate watched all hiding procedures in all conditions (and also monitored the dominant's visual access to these procedures) and so could potentially assess what the dominant had and had not seen (did and did not know) before the competition began. The second experiment was identical to two conditions of the first experiment (the subordinate knew whether the dominant either had or had not witnessed the hiding process) except that in the condition in which the dominant witnessed the hiding, we replaced the dominant individual with another before the competition began. This experiment thus investigated the subordinate's ability to keep track of what specific individuals had and had not seen (did or did not know). In a third experiment, the paradigm 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	Birthplace	Participation in experiment	Rearing history	Dominance rank
Group 1						
Bjorn	11	Male	Captivity	3	Mother/group	1
Peony	31	Female	Wild	1–3	Home-nursery	2
Borie	35	Female	Wild	1–3	Mother/group	3
Georgia	19	Female	Captivity	1	Mother/group	4
Renette	12	Female	Captivity	1–3	Mother/group	5
Natasha	12	Female	Captivity	1–3	Mother/group	6
Anja	19	Female	Captivity	1–3	Mother/group	7
Rita	12	Female	Captivity	1–3	Mother/group	8
Kate	10	Female	Captivity	2	Mother/group	9
Donna	9	Female	Captivity	1–3	Mother/group	10
Group 2						
Ericka	26	Female	Captivity	1–3	Home-nursery	1
Tai	32	Female	Wild	1, 3	Mother/group	1
Phineas	33	Male	Wild	1–3	Mother/group	2
Cynthia	19	Female	Captivity	1–3	Nursery/group	3
Barbi	23	Female	Captivity	2	Nursery/group	4

varied slightly so that the subordinate had to choose between two pieces of food, one of which the dominant had seen hidden and the other she had not.

Therefore, in all conditions the physical situation facing the subordinate was identical in the experimental and control conditions at the time of choice: either one or two pieces of food on its side of a barrier or barriers (out of sight of the competitor). The only difference was that in the immediate past the competitor either had or had not witnessed the food being placed or moved there. We were therefore not concerned with what chimpanzees know about what their competitor does and does not see in the present, but rather what their competitor has and has not seen in the immediate past, or, in one possible description of this epistemological situation, what its competitor does and does not know about the current situation. These nonverbal tests thus bear some resemblance to the verbal tests used by developmental psychologists to test children's understanding of: (1) seeing leads to knowing and (2) false belief (see Mitchell 1997 for a review). Whether these nonverbal versions should be interpreted in the same way is open to debate.

EXPERIMENT 1: DID SHE SEE IT HIDDEN OR MOVED?

In this experiment a subordinate was faced with the choice of either going or not going for a piece of food during competition with a dominant. In some conditions she had witnessed the dominant witnessing the final placement of the food, whereas in others she had witnessed that the dominant did not have visual access to the hiding procedures. Our hypothesis was that if the subordinates were sensitive to what others have or have not seen, they should more often approach and retrieve the food when the dominant was either

uninformed or misinformed (as opposed to informed) about its location.

Methods

Subjects

Twelve adult and subadult chimpanzees (mean age 21.6 years) housed in two social groups at the Yerkes Regional Primate Research Center Field Station participated in this experiment (see Table 1). Nine of the 12 subjects were subordinate to other individual(s) in their social group and contributed to the data set, while the remaining three chimpanzees (Peony, Tai and Ericka) were among the highest ranking in their respective groups and were used only in obtaining data from the other nine subordinate subjects. All subjects were captive born except Peony, Borie, Phineas and Tai. When not being tested, both groups had access to five indoor cages (3 × 3 × 3 m) as well as a large outdoor enclosure (24 × 24 × 30 m), which contained climbing structures and various objects such as balls, barrels, logs and tyres. During the period of testing all chimpanzees were fed twice daily, as usual, on a diet of fruit, vegetables and chow. Water was available ad libitum.

Subjects were tested in pairs consisting of a dominant and a subordinate individual ('dominant' and 'subordinate' in all studies refers solely to dyadic food dominance). The dominance hierarchy (see Table 1) had recently been established and used for both groups by Hare et al. (2000) and had been completed only a few days before the start of this experiment. All possible combinations of subordinate and dominant animals were tested except Rita–Georgia, Natasha–Borie, Tai–Ericka because our dyadic competition tests did not allow us to decide who was dominant (Rita and Natasha were subordinate to other females and were simply tested

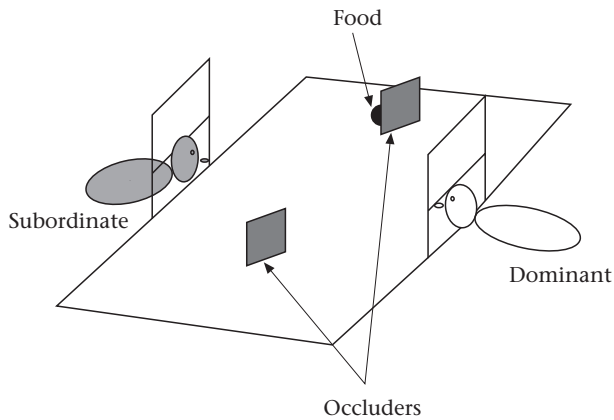


Figure 1. General experimental set-up in experiments 1–3.

twice with the next highest-ranking female). These combinations produced a total of 33 dyads.

Procedure

We used two opaque cloth bags (occluders) and small pieces of fruit (apples and bananas). A mechanical pincer mounted on a 3-m pole was used from outside the cage by two experimenters (E1 and E2) to place the fruit behind occluders. Testing took place in a row of three adjacent cages (see Fig. 1), with one animal in each of the extreme cages and the food in the middle cage. All three of the cages consisted of three concrete walls, a concrete floor, and a wire-mesh ceiling and fourth wall (facing a service hallway). There were guillotine doors between adjoining cages (0.6 m²), and also a door to the outdoor enclosure (which remained closed during testing).

For testing, all extraneous objects and food were removed from the cages. For each trial one piece of fruit was placed on the subordinate's side of one of the occluders. This side of food placement was counterbalanced across subjects. The occluders were placed 2 m apart, equidistant from the doors of each of the adjoining cages. To enhance the competitive nature of the situation from the point of view of the subordinate, the occluders were placed closer to the dominant's than to the subordinate's door (2 m from the subordinate's door and 1 m from the dominant's door).

There were four conditions based on the dominant's visual experience: Uninformed, Misinformed and their associated controls in which the dominant was informed (see below). Each dyad was tested in four sessions (with all 33 dyads tested in session 1 before moving on to session 2). In each session each dyad participated in one trial in each of the four conditions, for a total of 16 trials (four per condition) for each dyad across sessions. Each session also included two probe trials (not of experimental interest but simply designed to counteract some possible learning effects; see below). Order of conditions was counterbalanced across dyads within each session separately. All testing was completed within ca. 1 month.

Since subordinate animals were allowed to watch the entire baiting process in all conditions, the type of condition was determined by the dominant's experience

immediately before the competition. The four conditions were as follows.

Uninformed: the dominant's door remained closed as one piece of food was placed on the subordinate's side of one of the two occluders.

Uninformed (competitor informed): the dominant's door was left ajar as one piece of food was placed on the subordinate's side of one of the two occluders. (The subjects could thus potentially see one another looking.)

Misinformed: the dominant's door was open as one piece of food was placed on the subordinate's side of one of the two occluders (subjects could thus see one another looking). Then the dominant's door was closed, and after 5–10 s, the food was moved to the subordinate's side of the second occluder.

Control Misinformed (competitor informed): the dominant's door was left ajar as one piece of food was placed on the subordinate's side of one of the two occluders (subjects could thus see one another looking). Then, after 5–10 s and while the dominant watched (and the subordinate could see this), the food was moved to the subordinate's side of the second occluder.

Throughout the hiding process, the subordinate's door was open 15 cm whereas the dominant's door was either open or closed depending on the condition. Before the subordinate's door was raised, thus allowing her to enter the middle cage, we closed the dominant's door, regardless of whether it had been open before, and it remained closed until the subordinate's hand first touched the floor of the middle cage. (If the subordinate had not entered the cage after 30 s, the dominant was allowed to enter.) This was done to eliminate the possibility that the subordinate was simply reacting to the dominant's behaviour or orientation in the middle cage (Hare et al. 2000). Thus, the subordinate was forced to make a choice before she could observe the dominant making her choice.

To make certain that this procedure did not make the subordinates overconfident (i.e. assume they could go for the food indiscriminately since they always had a headstart) two probe trials per session were included (randomly interspersed). In these probe trials the dominant's door was left ajar and the piece of food was placed in the open, near (as opposed to on the subordinate's side of) one of the occluders, and both animals were released simultaneously. Therefore, these probe trials made it difficult for subordinates to predict when they would or would not have a headstart.

Scoring and data analysis

In each trial E1 and E2 decided together which subject had obtained the piece of food (i.e. who was eating it at the end of a trial). As in Hare et al. (2000), this determination was completely unambiguous in every case, and so reliability assessments were deemed unnecessary (once subordinates were in possession of food, dominants no longer tried to obtain it). We also scored whether the subordinate and the dominant subjects approached the occluders inside the cage once we raised the doors. We

distinguished three levels of approach: no approach, half approach and full approach. We scored no approach when the subject remained in her cage and did not enter or touch the floor of the middle cage. In a half approach the subject entered the middle cage or touched its floor but stopped halfway between the door and the occluders. We drew a line halfway between the door and the occluders parallel to the door to help E1 and E2 make this determination. Finally, we scored a full approach when the subject either stepped on the line or moved beyond it in the direction of the occluders. Again, the determination of the level of approach was unambiguous.

Analyses focused in all cases on the subordinate. Because different individuals were subordinate to different numbers of other individuals, different individuals participated as subjects in different numbers of trials. Consequently, we gave each individual a single score in each condition by computing a proportion. For example, a given subject might be paired with three different dominants, giving her 12 trials in each condition. In this case she would receive a score out of 12 (e.g. 6/12 or 0.50) for each condition. Nonparametric statistical tests were used in all cases; tests were one tailed unless indicated otherwise.

Results

Figure 2a shows the percentage of food pieces obtained by subordinate subjects in all four conditions. Pairwise comparisons were made between the Uninformed condition and its control and the Misinformed condition and its control. As predicted, subordinate subjects retrieved a significantly larger percentage of food when dominants lacked accurate information about the location of food (Wilcoxon test: Uninformed versus Control Uninformed: $T=36$, $N=8$, $P<0.01$; Misinformed versus Control Misinformed: $T=36$, $N=8$, $P<0.01$). In none of the conditions was there a difference across sessions, arguing against learning as a major factor (Friedman tests: Uninformed $\chi^2_3=2.1$, $N=9$, NS; Control Uninformed: $\chi^2_3=1.17$, $N=9$, NS; Misinformed $\chi^2_3=0.83$, $N=9$, NS; Control Misinformed: $\chi^2_3=3.9$, $N=9$, NS; all tests two tailed).

The percentage of trials in which subordinates chose not to approach the occluders fully (i.e. combining no approaches and half approaches) was used as an additional measure to determine whether subjects showed sensitivity to what their competitor had or had not seen during baiting. If subjects were sensitive to their competitor's visual access, they should refrain from approaching the occluders more often during the two control conditions in which dominants knew the location of the food. Subordinate subjects chose not to approach the occluders fully more often in the control condition than in the Uninformed condition (Wilcoxon test: $T=36$, $N=8$, $P<0.01$). Although six out of seven subjects also chose not to approach more often in the control condition than in the Misinformed condition, this difference did not reach significance (Wilcoxon test: $T=21.5$, $N=7$, $P=0.109$). One especially striking finding was that in some trials subordinate subjects chose to

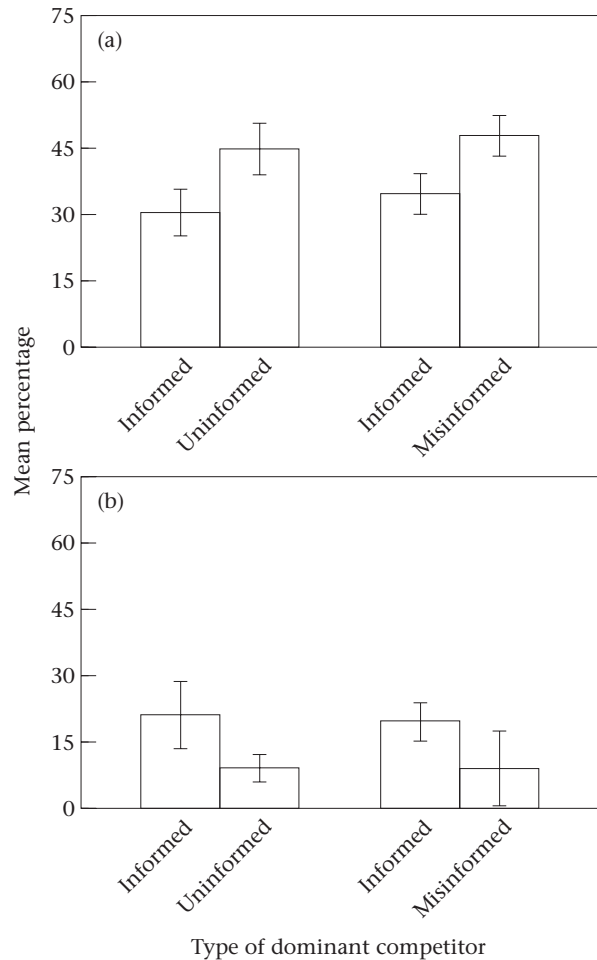


Figure 2. Mean percentage \pm SE of (a) pieces of food obtained by subordinate subjects and (b) trials in which subordinate subjects chose not to approach as a function of whether the dominant competitor was informed, uninformed, or misinformed about the location of the food in experiment 1. In informed trials dominant individuals witnessed the experimenter hiding food behind one of the occluders whereas in uninformed trials they could not see the baiting procedure. In misinformed trials, dominants witnessed the experimenter hiding food behind one of the occluders, and once the dominant's visual access was blocked, the experimenter switched the food from its original location to the other occluder.

remain in their own cage for 30 s even though they had unrestricted access to the middle cage. Restricting our analyses only to no approaches produced analogous results. Figure 2b shows the percentage of trials in which subjects chose not to approach in each test. Subordinate subjects chose to remain in their own cage significantly more often in the control condition than in the Uninformed condition (Wilcoxon test: $T=33$, $N=8$, $P<0.05$). There was also a nonsignificant trend in this direction for the comparison between the control and Misinformed condition (Wilcoxon test: $T=10$, $N=4$, $P=0.063$).

Finally, we assessed whether dominant competitors behaved differently depending on their experience, for instance, by choosing not to approach more often when they had not seen food being placed. There were

no significant differences between experimental and control conditions in either the Informed–Uninformed (Wilcoxon test: $T=20.5$, $N=7$, NS, two tailed) or the Informed–Misinformed test (Wilcoxon test: $T=5.5$, $N=4$, NS, two tailed). Overall, dominants did not approach during 11% of the experimental trials compared to 7.6% in control trials. This suggests that dominants were active competitors equally in both types of conditions (because they knew in all conditions that there was food somewhere).

Discussion

In this experiment the perceptual situation facing the subordinate when she made her choice was the same in all four conditions: she could see two barriers, a piece of food on her side of one of them, and a closed door across the room. What varied between conditions was what she had experienced prior to that moment of choice. In the two control conditions she had witnessed the dominant looking under the door as food was being either hidden or moved to a new location, whereas in the two experimental conditions she had witnessed the dominant's closed door as food was either hidden or moved to a new location. What subordinates then chose to do was clear: they chose to go for the food more often, and they obtained it more often, when their dominant competitor had not seen it hidden or moved. The most obvious interpretation of this differential behaviour is that the subordinate knew from her experience of the hiding process in each condition whether or not her dominant competitor had seen, as she had seen, where the food had been placed.

These results are not easily explained by any kind of learning since the subjects' performance did not change in any detectable way over the four sessions. This means that whatever information subordinates gained by watching the hiding process, and monitoring the dominant's visual access during it, involved something deeper than any kind of learned discriminative cue. These results also cannot be easily explained by any kind of behavioural cueing. At the time of the subordinate's choice the dominant's door was closed and so there were no behavioural cues to be seen, and the subordinate had to make her choice before the dominant's door was opened. Indeed, most subordinates on some trials in the control conditions (when the dominant had seen the hiding or moving) chose to stay in their cage for the entire 30 s, simply staring across at the dominant's closed door. Another possibility is that subordinates may have learned over trials that the dominant's behaviour varied between conditions. For example, subordinates might have learned that dominants were less likely to approach if they had not seen the baiting. This hypothesis, however, was not supported by the data since dominants approached on a comparable number of trials in all conditions.

There is one other hypothesis (and a corollary) that must be addressed. The hypothesis is that during the hiding process the dominant looked intimidating as the food was being hidden (in those conditions in which she

saw food being hidden) which made the subordinate timid about going for the food at the time of choice. We may call this the intimidation hypothesis. This hypothesis is viable when comparing the Uninformed condition and its associated control condition, since in the latter the subordinate witnessed the dominant witnessing the hiding (and thus had the opportunity to be intimidated) but this was not the case in the Uninformed condition (when the dominant's door was closed throughout). So, under the intimidation hypothesis, the subordinates should not go for the food in the control condition but should go for the food in the Uninformed condition, and this is exactly what they did. However, the intimidation hypothesis cannot explain the difference between the Misinformed condition and its associated control condition. Subordinates watched dominants witnessing the hiding process in both of these conditions, and so they should have been equally intimidated in both. But this was not the case, as they went for the food more often in the Misinformed condition. We therefore conclude that the intimidation hypothesis is not a viable explanation of our results.

A corollary hypothesis is as follows: when the dominant witnesses the hiding she watches the food and then acts in an intimidating manner towards the place she saw it disappear; that is to say, by staring at it she marks it as 'mine'. On the surface, this hypothesis seems plausible since subjects tended to avoid the food that the dominant saw hidden in the Misinformed control, and they tended to go for the food in the new location after it had been moved in the Misinformed condition, a location that the dominant could not have looked at intimidatingly since no food was ever placed there while she was looking. However, Hare et al. (2000; experiment 4b) were also concerned with this hypothesis and so ran a control study designed specifically to test it. They set up a situation in which the dominant could see the food but the subordinate could not (the food was on the dominant's side of one of the occluders), and they then released the subordinate into the middle cage to see if something in the dominant's behaviour might serve either to attract her to or to repel her from the location of the hidden food. The subordinates chose randomly, apparently being neither intimidated nor attracted by anything the dominant was doing in the direction of the food (see also Itakura et al. 1999).

EXPERIMENT 2: WHO SAW IT HIDDEN?

In the previous experiment subordinate chimpanzees behaved differently depending on what their dominant competitor had or had not seen during baiting. If their behavioural choices in that experiment were indeed a reflection of an underlying social-cognitive strategy, as opposed to some simple learned cue, then we should expect them to be able to use this strategy in a flexible manner in novel situations, and without taking numerous trials in the new situation to adapt. In this second experiment, therefore, we presented subordinates with a novel situation that required them to adjust their strategy. As in the two control (informed) conditions of

the first experiment, food was placed on the subordinate's side of one of two occluders and the subordinate witnessed both the baiting procedure and her dominant competitor's witnessing of the baiting procedure. The critical manipulation was that on some trials, after the dominant had witnessed the baiting, she was replaced with a new dominant individual that had not witnessed the baiting. This new individual had been out of the experimental area completely when the baiting took place, and so could have no information about where the food was hidden. If chimpanzees have some understanding of what others have seen, as suggested by the previous experiment, then they should immediately go for the food more often when they compete against a new (uninformed) dominant rather than the old (informed) one.

Methods

Subjects

Twelve adult and subadult chimpanzees (mean age 20.1 years) participated in this experiment (see Table 1). Eight of the 12 subjects were used as subordinates and contributed to the data set. Two of those eight subordinates had not participated in experiment 1.

Procedure

In this experiment each of the eight subordinate individuals was tested with a pair of dominant competitors (i.e. not all combinations were used). Each subordinate participated in two sessions of four trials (for a total of eight trials per subject). Within each session a subordinate competed against each of its two dominant competitors twice. In one condition (Same) the subordinate competed only against the dominant who had witnessed the baiting, whereas in the other condition (Switch) she competed only against the dominant who did not witness the baiting. Each subject alternated between experimental conditions, with the nature of the initial condition counterbalanced across subjects. All testing was completed within 1 week.

We used the same general food competition paradigm as in experiment 1 (Uninformed versus Uninformed Control). In this case, however, there were two dominants (D1 and D2) who were housed separately in two adjoining cages on one side of the middle cage, with the subordinate in the cage on the other side of the middle cage. The layout of the occluders and placement of food were as in experiment 1 (Fig. 1).

For each trial, a subordinate subject witnessed food being placed on her side of one of two occluders, and she witnessed a dominant witnessing this hiding (as in the two control conditions of experiment 1). After the food was hidden, the dominant's door was closed and remained closed in both conditions during a 90-s delay. What happened during this 90-s period depended on the experimental condition.

Switched Competitor: during the 90-s period experimenters replaced D1 with D2, the naïve dominant who was in the adjoining cage. Offering food to the

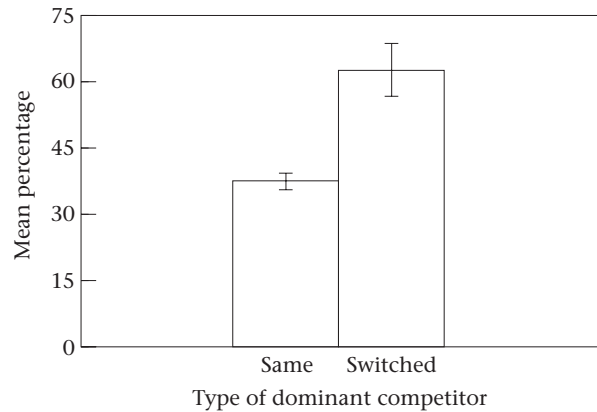


Figure 3. Mean percentage (\pm SE) of pieces of food obtained by subordinate subjects in experiment 2 as a function of whether the dominant competitor was the one who had witnessed the baiting (same) or was a different individual (switched). In same trials, the subordinate competed against the same dominant who had witnessed the baiting (i.e. the dominant knew where the food was) whereas in switch trials the subordinate competed against a dominant who had not witnessed the baiting (i.e. did not know where the food was).

most dominant subject of the D1–D2 pair in the cage occupied by the less dominant subject made the most dominant subject change positions. We then offered food to the less dominant animal (while distracting the other) in the empty cage until she moved to complete the change-over. Then the dominant's door was raised 15 cm to show the subordinate that D1 was no longer present and that D2 (who did not witness the baiting) was now her competitor.

Same Competitor (control): D1 remained in her cage during the 90-s delay, and then her door was opened 15 cm again to show the subordinate that D1 (who had witnessed the baiting) was still her competitor.

After the subordinate had been shown her competitor, the dominant's door was closed and the subordinate was released while the dominant competitor's release was delayed until the subordinate began to enter the cage (as in experiment 1). If the subordinate did not enter the cage within 30 s, the dominant was released (as in experiment 1). Scoring and analysis were identical to those used in experiment 1.

Results

Figure 3 shows the percentage of pieces of food obtained by the subordinate subjects in each of the two conditions. As predicted, subordinate subjects retrieved a significantly larger percentage of food when they competed in the Switched condition, that is, with a competitor they knew had not seen the baiting (Wilcoxon test: $T=28$, $N=7$, $P<0.01$). There were no significant differences in subject performance across the two sessions in either condition, showing that this difference was not due to learning over trials (Wilcoxon test: Same

Competitor: $T=18$, $N=6$, NS; Switched Competitor: $T=8.5$, $N=5$, NS, two tailed in both tests).

We also looked at the subjects' tendency to approach the food to determine whether they were showing sensitivity to which dominant competitor they were facing. Owing to the small number of trials involved, we scored as 'no approaches' those cases in which subjects entered the cage but did not cross the halfway line between the door and the occluders (there was a line drawn across the floor of the cage to help E1 and E2 make this determination). Five subjects remained behind the halfway point more often in the Same Competitor condition while only one subject remained behind the line more often in the Switched Competitor condition, but this difference was not statistically significant (Wilcoxon test: $T=15$, $N=6$, NS). As was the case in experiment 1, there were no significant differences in the dominants' approach behaviour across conditions (Wilcoxon test: $T=6$, $N=3$, NS, two tailed).

Discussion

The results of this experiment corroborate and extend those of experiment 1. Subordinates were again more likely to approach and retrieve food when their dominant competitor had not witnessed its placement. This finding is especially robust since all subjects showed the same response pattern immediately. Therefore, whatever subjects from experiment 1 might have brought with them into this experiment, they were quickly able to adapt it to this completely novel situation (this study thus represents a case of successful triangulation in the terms of Heyes 1993). Both new subjects who did not participate in experiment 1 also showed a preference for retrieving food in the Switched Competitor condition. Again in this experiment, learning cannot account for preferences since there were no differences between the two rounds of trials for either condition. Also, these results provide a kind of generalized control for those of experiment 1, since they in effect rule out the possibility that chimpanzees automatically responded to certain spatial and temporal arrangements of the baiting procedures in that study, since in this second experiment the same arrangements and procedures led to different results, the only difference being the personal identity of the competitor.

Perhaps most importantly, this experiment extended the results of the previous one by showing that chimpanzees can keep track of which individuals have witnessed a significant event and which have not. It thus seems that chimpanzees can combine their well-attested ability to recognize individuals (see Tomasello & Call 1997 for a review) with their social-cognitive skill to determine whether someone has or has not witnessed an important event. Subordinates in our study apparently did not think that the two dominants had exchanged information during the 90-s delay (initially suggested by Menzel 1973), although this hypothesis might be better tested in a different experimental arrangement.

EXPERIMENT 3: WHICH PIECE DID SHE SEE HIDDEN?

The two previous experiments are consistent with the hypothesis that chimpanzees are able to recognize and take advantage of what others have or have not seen. We designed experiment 3 to examine the flexibility of this ability. In this experiment subordinates were required to remember what a dominant competitor had witnessed during the baiting of two pieces of food. Subordinates always witnessed the baiting of both pieces of food, but dominants saw only one piece of food being hidden (and they were either Uninformed or Misinformed about the location of the second piece of food). We predicted that subordinates would preferentially retrieve those pieces of food about whose location the dominant competitors were either Uninformed or Misinformed.

Methods

Subjects

Twelve adult and subadult chimpanzees (mean age 20.9 years) participated in this experiment (see Table 1). Nine of the 12 subjects were used as subordinates and contributed to the data set. The other four were used only as dominants to obtain data from the nine subordinate subjects. All possible combinations of subordinate and dominant animals were tested except Natasha–Borie and Tai–Ericka because our dyadic competition tests did not allow us to decide who was dominant (Natasha was a subordinate and was tested twice with the next highest-ranking female instead). In addition, a new subject (Bjorn) was used as a dominant for Peony only (the highest-ranking female in group 1 who had never played the role of subordinate in any experiment). These combinations created a total of 27 dyads. (This experiment was actually completed prior to experiment 2.)

Procedure

Each dyad was tested in two sessions, each of which contained six trials (a total of 12 trials per dyad), with two probe trials in each session as well. As in experiment 1, order of conditions was counterbalanced across dyads within each session separately. All testing was completed within 2 weeks.

Subjects were tested in the same general food competition paradigm and the same general experimental conditions as in experiment 1. The difference was that we used what we called two-piece versions of each condition. That is, whereas in the first experiment the subject had to decide in each condition whether to go for the one piece of food, in experiment 3 we arranged it so that there were always two pieces of food and the dominant sometimes saw only one of them either hidden or moved. The subject then had to choose in every trial which of two pieces of food it should go for. As in experiment 1, the subordinate was able to witness all baiting procedures in all conditions. The four conditions were as follows.

Uninformed: the dominant's door was left ajar and the experimenter placed one piece of food on the subordinate's side of one of the two occluders. Then the dominant's door was closed and a second piece of food was placed on the subordinate's side of the other occluder.

Control Uninformed (competitor informed): the dominant's door was left ajar as first one piece of food was placed on the subordinate's side of one of the two occluders, and then a second piece of food was placed on the subordinate's side of the other occluder.

Misinformed: the dominant's door was left ajar and two pieces of food were hidden on the subordinate's side of one of the two occluders (both behind the same occluder). Then the dominant's door was closed. Then, after 5–10 s, one of the pieces of food was moved to the subordinate's side of the other occluder.

Control Misinformed (competitor informed): the dominant's door was left ajar and two pieces of food were hidden on the subordinate's side of one of the two occluders (both behind the same occluder). Then, after 5–10 s, one of the pieces of food was moved to the subordinate's side of the other occluder while both chimpanzees were watching.

All of the other procedures were as in experiment 1; in particular the subordinate was always given a small head-start and the dominant's door was always closed at the time of her choice. Scoring and analysis were identical to those used in the previous experiments. Again to guard against counterproductive learning strategies, we used probe trails (two per session, randomly interspersed). The probes were designed to solve the problem created by the fact that at the time of choice in all four conditions both barriers were baited. If these were the only conditions, the baiting procedures could have become irrelevant for subjects since they could never choose incorrectly (unlike experiments 1 and 2). Therefore, two types of probe trials were used, one in which both subjects watched as only one piece of food was hidden on the subordinate's side of a barrier and one in which both subjects watched as two pieces were hidden on the subordinate's side of one of the barriers.

Results

In this experiment, subordinates did not retrieve more food when the dominant had no knowledge of one piece's location (Wilcoxon test: Uninformed versus Control Uninformed: $T=22$, $N=7$, NS; Misinformed versus Control Misinformed: $T=19.5$, $N=8$, NS; Fig. 4). Of crucial importance was which piece of food subordinates retrieved in each of the two experimental conditions (i.e. the one the dominant had seen hidden or the one she had not seen hidden). Subordinates showed no preference in this regard in either the Uninformed (Wilcoxon test: $T=18.5$, $N=7$, NS; Fig. 5) or the Misinformed condition (Wilcoxon test: $T=11$, $N=5$, NS; Fig. 5), although the difference is in the predicted direction in both cases.

As in the other experiments, we also analysed subordinate approaches. The results were mixed. As

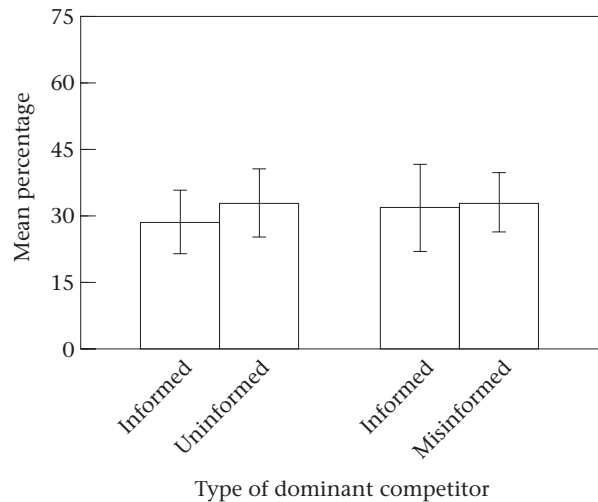


Figure 4. Mean percentage \pm SE of pieces of food obtained by subordinate subjects in experiment 3 as a function of whether the dominant was informed, uninformed, or misinformed about the location of the two pieces of food. In informed trials dominant individuals witnessed the experimenter placing one piece of food behind each occluder whereas in uninformed trials they witnessed the placement of only one of the pieces, the other being introduced when she was unable to see the baiting. In misinformed trials, dominants witnessed the experimenter placing two pieces of food behind one of the occluders, and once the dominant's visual access was blocked, the experimenter moved one of the two pieces from its original location to the other occluder.

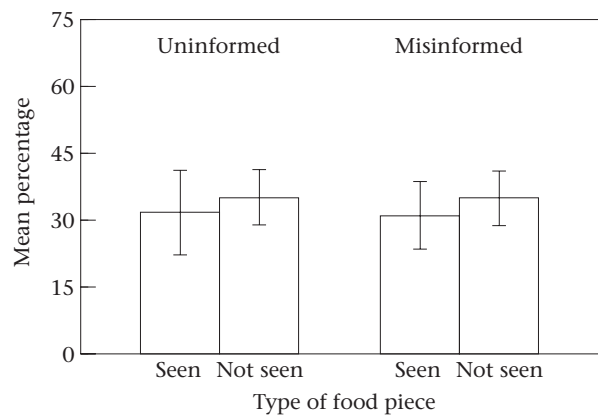


Figure 5. Mean percentage \pm SE of the two pieces of food obtained by subordinate subjects in experiment 3. The dominant competitor saw one piece of food being hidden (seen) and was uninformed or misinformed about the location of the other (not seen).

predicted, subordinates chose not to approach more often in the Control Misinformed (12.5%) than the Misinformed condition (3.2%), although this difference did not reach significance (Wilcoxon test: $T=14$, $N=5$, $P=0.063$). On the other hand, there were no significant differences between the Uninformed condition and the Uninformed Control in how often subjects chose not to approach (Wilcoxon test: $T=5$, $N=3$, NS; Uninformed=2.5%, Control Uninformed=7.4%). We also assessed approaches using the 'halfway to the food' criterion of experiment 1. No significant differences were

found in subjects' tendency to approach pieces of food that their dominant competitor either had or had not seen.

In this experiment the approaches of dominants after release may be relevant to the behaviour of subordinates. From the very beginning of the experiment we noted that a number of dominants were using a new strategy against subordinates. Regardless of what they had seen during baiting, dominants began to approach the occluder that subordinates approached first (effectively 'shadowing' the subordinates' movements). Therefore, throughout this experiment we recorded in which trials dominants shadowed subordinates. Out of the 10 subjects who played the role of dominant, eight females frequently shadowed while the two males never did. Dominants shadowed in 34% of trials, with the mean rate of shadowing by the eight females being 43% of trials (range 19–88% of trials).

Discussion

Unlike the previous two, in this experiment there was little evidence to support the hypothesis that subordinates were sensitive to what dominants had seen during baiting. Only subordinates' tendencies to approach less in the Control Uninformed condition (when dominants witnessed both pieces of food being hidden) were consistent with the previous findings. These inconsistent results might be explained in one of three ways.

First, chimpanzees may not have the ability to know what others have and have not seen and to judge how this might affect their behaviour, and this experiment validly reflects that lack of skill. To maintain this hypothesis we would have to claim that this experiment is somehow a better test of chimpanzee social-cognitive skills than the first two; we might base this judgement on the fact that in this experiment chimpanzees had to make an active choice between two courses of action rather than simply deciding to go or not to go, as in the first two. It seems unlikely to us, however, that this experiment is the more valid one; rather, it is more likely that it created additional problems for the chimpanzees unrelated to their social-cognitive skills.

Second, the addition of the second piece of food may have changed the incentive structure for the competitors. Since there was food behind each of the barriers on each experimental trial, the competitive dimension of the situation might have been too greatly diminished. Although we used probe trials, there might have been too few probes or they might not have worked as planned. Some evidence for this possibility is the fact that subordinates retrieved the majority of pieces of food in both types of probe trials (54% overall), presumably because they had learned over all the experiments to use their headstart more effectively, and so dominants might not have been rewarded enough in these probe trials for them to have an impact on their own retrieval behaviour. A related problem was the shadowing strategy that many dominants developed. Although this strategy might also have been successfully used in the previous experiments,

in fact it was not (we did not code for it systematically in previous experiments simply because it was not present); presumably it was learned over time by some individuals as an 'easy' way to get food. The problem shadowing creates, of course, is that if subordinates are going to be shadowed on potentially every trial, it matters little to which occluder they go when trying to avoid the dominant; what dominants did or did not see was, in effect, irrelevant since it did not affect their behaviour.

Finally, chimpanzees' behaviour in this experiment may reflect an inability to keep track of what others have seen with respect to two significant events; this may simply be an information overload that reflects a genuine cognitive limitation but not a limitation in judging what others have and have not seen. In this regard, note that in the traditional 'change location' false belief tests commonly used with human children (Wimmer & Perner 1983), subjects need only track another person's belief about a single object, the same as in experiments 1 and 2. Chimpanzees may track what their competitor has seen when two objects are hidden, but simply cannot organize this amount of information in a way that enables them to integrate it into their behavioural strategy.

It would clearly be a strong addition to our findings to have a valid study in this general food competition paradigm in which the subject has to make an active choice between two pieces of food, one whose location she knows the competitor knows and one whose location she knows the competitor does not know. However, our conclusion for the moment is that this set-up in its current form is not a valid test, since it changes the incentive structure of the competition and may, in addition, place excessive information-processing demands on subjects. Constructing a valid two-piece choice version of this task thus remains a goal for future research.

GENERAL DISCUSSION

Our results represent the clearest demonstration to date that chimpanzees know what individual groupmates do and do not 'know', that is, what individual groupmates have and have not seen in the immediate past. Other experimental approaches have either found negative results or found positive results only after extensive training (e.g. Povinelli et al. 1990, 1994; Call & Tomasello 1999; Call et al. 2000). We attribute the positive results in our study to an experimental situation that was more naturalistic than previous ones. Thus, unlike previous experimental situations, it did not require chimpanzees to communicate with humans about the location of a monopolizable food resource (which is a very unnatural situation for them) or to be trained in how to behave in a completely novel task. With no training or human intervention, chimpanzees demonstrated their social-cognitive skills in a food competition situation among themselves. Our failure to find positive results in experiment 3, requiring the subjects to compete over two pieces of food, only one of whose locations was mutually known, has a ready explanation in terms of the different behavioural strategies that this set-up engendered in

the dominant competitor (and perhaps the extra information-processing load it placed on the subordinate competitor).

The two tasks of experiment 1 bear some resemblance to tasks that have been used with human children and considered as indicators that children understand that: (1) seeing leads to knowing; and (2) other persons can have false beliefs (Mitchell 1997). But ours are nonverbal tasks and so their interpretation is more difficult; we therefore prefer to remain cautious. From this cautious perspective, here is what we believe our results, in combination with other recent studies, show.

(1) Chimpanzees know what other individuals do and do not see. Thus, they reliably follow the gaze direction of others (Tomasello et al. 1998); they do this around barriers and past distracters (which suggests that they are doing much more than just using head direction as a discriminative cue; Tomasello et al. 1999); and they reliably use information about what conspecifics can and cannot see in a food competition situation (even showing knowledge that transparent barriers do not block the visual access of others; Hare et al. 2000).

(2) Chimpanzees can recall what a conspecific has and has not seen in the immediate past (current experiment 1), and this recall is associated with specific individuals (experiment 2). Chimpanzees integrate this recall about what specific individuals have and have not seen into their behavioural decision making in competitive situations (this study).

For some theorists, this profile is just another way of saying that chimpanzees know what others know. But the word 'know' is a multifaceted word, and our view is that our results show that chimpanzees know about some aspects of what others know, but perhaps not about other aspects. The problem is that in many theoretical discussions of these issues, only two alternatives are presented: chimpanzees either have a 'theory of mind' like that of humans' (i.e. they engage in mental state attribution) or they simply learn by blind behavioural conditioning (e.g. Byrne 1995; Heyes 1998, but see Byrne & Whiten 1992). But we believe that there is a middle ground, or as we have called it 'an explanation of the third kind' (Tomasello & Call 1997; Call & Tomasello, *in press*; see also Whiten 1996). This third way recognizes the widely accepted fact that chimpanzees have insight into some physical problems, which enables them to develop intelligent problem-solving strategies involving tool use and the like, and then simply extends this to the social domain; chimpanzees have insight into some social problems, which enables them to develop intelligent problem-solving strategies in this domain as well. But this does not necessarily mean that chimpanzees have human-like social-cognitive skills ('theory of mind') in which they understand such things as: (1) others can have different perspectives on the same object I am now perceiving (e.g. from a different angle); (2) I can simulate the visual experience of others by imagining how I would see things if I were in their place; and (3) others have beliefs about things that may differ from my own and from reality. Indeed, chimpanzees show

no evidence of such human-like, social-cognitive understanding in a variety of other studies of their social cognition (see Tomasello & Call 1997, for a review).

One way of summarizing our third-way hypothesis is to say that chimpanzees are able to engage in Level 1 perspective taking (knowing that others can see things that I cannot and vice versa) but not Level 2 perspective taking (knowing precisely what others see, including that they see the same thing I do but from a different perspective; Flavell 1985, 1992). In the current task, for example, they may employ a 'rewind strategy'. That is, they notice what their competitor sees and does not see as food is being hidden, and then, when the moment of decision comes, they 'rewind the tape' and act as if the competitor were currently looking at the scene. In this view, chimpanzee social cognition is based on a representational understanding of the behaviour of others, which permits them to do things like remember, foresee and communicatively manipulate the behaviour and social relationships of others. This cognitive machinery then enables them to react appropriately in social situations, and also to predict and influence their groupmates' behaviour in novel situations. But these skills are not unlimited. Chimpanzees may not recognize certain kinds of intentional or mental states, and they may have trouble in developing strategies in situations in which they must use their knowledge to imagine what another might see in some totally novel situation. For example, in our study it is unclear what subordinates would do if they were given the opportunity to manipulate a barrier so that it could either block the dominant's view or not before the trial begins. The main point is that we should be focused not on the yes-no question (do chimpanzees have a theory of mind?), but rather on a whole panoply of more nuanced questions concerning precisely what chimpanzees do and do not know about the psychological functioning of others (see also Whiten 1996).

Although informative in their own ways, previous studies that have asked chimpanzees to demonstrate their social-cognitive skills by communicating with humans, often in a task that requires much training, are apparently asking too much of them. These studies require chimpanzees to comprehend the communicative intentions of others, and to do this in a situation in which, for them, competition is a much more natural mode of interaction. Most chimpanzees probably go their whole lives without having anyone altruistically point out for them the location of a monopolizable piece of food in front of both of them (Hauser & Wrangham 1987; Hauser et al. 1993). Evolutionary theories of primate cognition stress the fact that primates exist within a complex social field and must constantly find new ways to compete against other individuals intent on reaching their own goals, or else they will not survive long enough to pass on their genes (Humphrey 1976, 1981; Krebs & Dawkins 1984; Byrne & Whiten 1988). It is therefore likely that primate social-cognitive abilities evolved to a large degree to allow individuals to outcompete competitors, and so it is in these kinds of settings that we are most likely to see these abilities expressed. In this regard,

domestic dogs, who have been under a completely different regime of selective pressures and rearing practices, which may have encouraged more skills of cooperation and communication with others, especially humans, perform much better than chimpanzees in an object choice task in which they must learn to read human behaviour as humans attempt to communicate to them the location of a hidden, monopolizable food resource (Hare et al. 1998; Miklósi et al. 1998; Hare & Tomasello 1999). In attempting to design ecologically valid experiments of primate cognition and social cognition, therefore, researchers must always take into account not only their current behavioural skills and propensities but also the functional contexts within which their cognitive abilities have most likely evolved.

Acknowledgments

This investigation was supported in part by a grant from the National Science Foundation to M.T. (IBN-9507418) and in part by NIH grant RR-00165 from the National Center for Research Resources to the Yerkes Regional Primate Research Center. The Yerkes Center is fully accredited by the American Association of Laboratory Animal Care. We thank Katja Liebal and Melissa Emory for help with data collection and Malinda Carpenter, Signe Preuschoft, Marc Hauser, Andy Whiten, Julia Fischer and Richard Wrangham for valuable comments on the manuscript.

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