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Chimpanzees are more skilful in competitive than in cooperative cognitive tasks

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In a series of four experiments, chimpanzees, *Pan troglodytes*, were given two cognitive tasks, an object choice task and a discrimination task (based on location), each in the context of either cooperation or competition. In both tasks chimpanzees performed more skilfully when competing than when cooperating, with some evidence that competition with conspecifics was especially facilitatory in the discrimination location task. This is the first study to demonstrate a facilitative cognitive effect for competition in a single experimental paradigm. We suggest that chimpanzee cognitive evolution is best understood in its socioecological context.

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There is currently a large discrepancy in the findings of different studies of social cognition in chimpanzees, *Pan troglodytes*. On the one hand, research has shown that chimpanzees know what other individuals can and cannot see and even what others have and have not seen in the immediate past (Hare et al. 2000, 2001). Furthermore, in some situations they can also formulate behavioural strategies to manipulate actively what others can and cannot see by hiding their own approach to contested food (B. Hare, J. Call & M. Tomasello, unpublished data). In all these studies chimpanzees displayed their understanding and skills from the very first trials of testing, with no training from humans required. On the basis of these studies, therefore, we might conclude that chimpanzees understand some of the psychological states of others, and they can even take measures to manipulate those states when it is to their own advantage.

On the other hand, in a different experimental paradigm chimpanzees show surprisingly weak social-cognitive skills. Of special importance is the so-called object choice paradigm. In this paradigm subjects are presented with two opaque containers, only one of which contains food (and they know this, and also that they can choose only one). A human experimenter then looks or points continuously at the container with food hidden inside. In Call et al.'s (1998) study, not one of six chimpanzees used this cue to find the food. Tomasello et al. (1997) and Call et al. (2000) provided chimpanzees with several other types of visual–gestural cues in this same paradigm and also found mostly negative results. Povinelli et al. (1999) found that some chimpanzees could learn to use similar cues after several dozen trials, but they also showed in various ways that this was for them only a learned behavioural cue, not an indicator of the visual experience of others; for example, when the experimenter turned his head in the direction of the baited container but looked to the ceiling, subjects chose the correct container just as often as if the experimenter looked directly at it. Itakura et al. (1999) used a trained chimpanzee conspecific to give the gaze direction cue, but still found mostly negative results. Other primate species also take dozens or scores of trials to learn to use human social cues in the object choice paradigm (Anderson et al. 1995; Vick et al. 2001; Neiworth et al. 2002). In addition, once primates learn to use one social cue to find hidden food in this task, they do not readily generalize to either a new social cue or a slight change in procedure using the same cue (Povinelli et al. 1997; Tomasello et al. 1997). And it is not the case that the object choice paradigm is simply confusing for animals. Many studies show that domestic dogs, *Canis familiaris*, are very skilful in this task, successfully using a variety of different social cues produced by both humans and other dogs, with no training from humans in this context (e.g. Hare et al. 1998; Miklosi et al. 1998; Hare & Tomasello 1999). Indeed, in the one

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study in which chimpanzees and dogs were directly compared, the dogs were much more skilful, and this included puppies with little human experience (Hare et al. 2002).

Chimpanzees' struggles in the object choice paradigm are thus surprising, given their skills in some other experimental paradigms. Their struggles are also surprising given that many evolutionary theorists have noted that primates have an unusually complex socioecology that should result in strong selection for social-cognitive skills in general (e.g. Byrne & Whiten 1988). One hypothesis for explaining this puzzle comes from considering more precisely the kinds of social problems that group-living primates have faced over evolutionary history and in daily life. For example, primates avoid giving food calls when they discover monopolizable food, but instead are more likely to call when food is shareable (Dittus 1984; Hauser et al. 1993; Hauser 1997). In addition, primates have never been observed to indicate the location of hidden food to conspecifics overtly by gesturing towards it (Menzel & Halperin 1975; Coussi-Korbel 1994; Hirata & Matsuzawa 2001). These observations highlight the fact that group-living primates are constantly competing against conspecifics for access to food and mates, so much so that it has been difficult to explain why primates live in social groups at all (Wrangham 1980; Sterck et al. 1997). It thus follows that selection has favoured individuals capable of outcompeting conspecifics.

Based on this line of reasoning, Hare (2001) proposed the competitive cognition hypothesis to explain the seemingly inconsistent pattern of results in experimental studies of chimpanzee (and perhaps other primate) cognition. The hypothesis predicts that chimpanzees will demonstrate the greatest skill or motivation in competitive, rather than in cooperative, cognitive tasks (see also Tomasello et al. 2003). The fact is that the paradigms in which chimpanzee social-cognitive skills have been most impressively displayed are all basically competitive in nature (Hare et al. 2000, 2001). In contrast, in standard object choice tasks a cooperative human altruistically communicates to subjects the location of a monopolizable food resource, a situation unlike those for which primate cognition is naturally adapted. Following this line of evolutionary reasoning, it is also not surprising that domestic dogs, which have been selected for cooperating and communicating with humans, perform best in cooperative–communicative cognitive paradigms such as the traditional object choice task.

Although such comparisons across studies are suggestive of a difference in chimpanzees' performance in cooperative and competitive tasks, what is needed is a single task setting within which chimpanzees experience social cues in either a cooperative or a competitive context. In the current study, therefore, we tested chimpanzees in the object choice paradigm in one of two ways. First, in some cases a human first established a cooperative relationship with a chimpanzee subject (e.g. by encouraging them in a friendly manner), and then later, in test trials, provided the cooperative–communicative cue of pointing to indicate the hidden food's location, all as in the standard object choice task. Second,

in other cases a human first established a competitive relationship with a chimpanzee subject (e.g. by obtaining contested food whenever he could and protesting when the subject got food), and then later, in test trials, tried unsuccessfully to reach one of the two opaque test containers in an attempt to obtain it before the subject. The physical movements of the human in these two cases were actually highly similar: in both cases he extended his arm towards the hidden food's location. However, in one case he was doing this in an attempt to help the subject locate the food, in which case the subject had to read his communicative intentions, whereas in the other case he was doing it in an attempt to get the food for himself, in which case the subject only had to infer the target of his reaching action. To try to establish in more detail some of the specific parameters affecting chimpanzees' performance in this new version of the object choice paradigm, we also tested them in a similar but different task involving simple discrimination (location) learning, also in both a competitive and a cooperative mode. Finally, in both the communication task and the discrimination location task, subjects competed both against a human and a conspecific, to see if the nature of the competitor made a difference.

EXPERIMENT 1

In experiment 1, we tested whether subjects would be more successful at finding food when they could exploit unintentional cues from a human competitor or when a human cooperator intentionally provided communicative cues. We predicted that the subjects who were introduced to the competitor would be more successful in using a social cue to locate hidden food than those who were introduced to a cooperator, even though both groups were provided with an almost identical cue (extended arm) to the location of the hidden food. Perhaps importantly, the subjects in this experiment had previously been tested for their ability to use the social cues of a cooperative–communicative human in a standard object choice task. There was no evidence from individual or group analyses that these subjects were capable of spontaneously finding hidden food when a human experimenter gazed at (oriented his eyes), looked at (oriented his face), or pointed to the hiding location containing the food (J. Barth, J. Call & M. Tomasello, unpublished data).

Methods

Subjects

Twelve chimpanzees participated in experiment 1 (Table 1 shows each subject's sex, age, rearing and test history). All the chimpanzees tested live at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo, Germany. The group consists of 18 individuals. During the day, they live in a 4000-m^2 outdoor area, and a 400-m^2 indoor area, both of which have many places for vertical climbing (both observable by the public). An enrichment programme introduces novel foraging apparatuses on a regular basis.

Table 1. Subject's sex, age, rearing and test history

Name	Sex	Age (years)	Rearing history	Test history*
Robert	Male	27	Nursery	2
Riet	Female	25	Nursery	1, 2
Fraukje	Female	26	Nursery	1, 2
Natasha	Female	22	Nursery	1, 2
Corry	Female	26	Nursery	2
Ulla	Female	25	Nursery	1
Frodo	Male	9	Mother	1, 2
Fifi	Female	9	Mother	1, 2
Sandra	Female	9	Mother	1, 2
Jahaga	Female	9	Mother	1, 2
Trudy	Female	9	Mother	1, 2
Patrick	Male	5	Mother	1, 2

*1: Subject participated in another study: J. Barth, J. Call & M. Tomasello, unpublished data; 2: subject participated in Hare et al. (2002).

During the night they sleep in a series of sleeping cages totalling approximately 150 m². Subjects were tested in one of two familiar test cages, each of which was approximately 40 m². The chimpanzees are fed various fruits, vegetables and cereals several times per day. They were not food deprived for testing, and water was available at all times throughout this and all subsequent experiments. Subjects could choose to stop participating at any time.
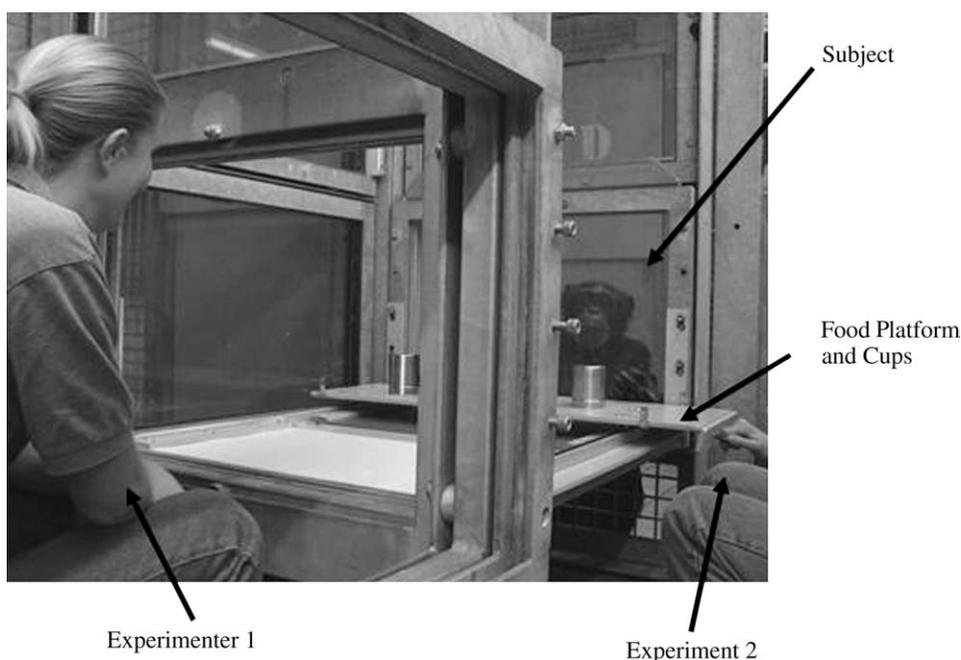
Apparatus

Figure 1 shows the experimental set-up. A wooden table (91×80 cm) with a sliding food platform was placed inside a test booth which included two Plexiglas test windows (71×60 cm). The sliding food platform (1×0.1 m) rolled in tracks cut into the top of the table and could slide across the table between the two test windows (90 cm). Two cups were attached to the sliding platform with hinges and were 50 cm apart. Two oval hand holes (10×3 cm) were cut into the subject's Plexiglas test window and allowed subjects to reach their fingers out so that they could retrieve food from one of the cups when the sliding platform was pushed forward. Experimenter 1 (E1) could sit across from the subject on one side of the test apparatus while experimenter 2 (E2) could slide the food platform between the subject and E1.

Procedure

Warm-up. First, all subjects were introduced to the apparatus. Once the subjects were seated in front of the test window with the two oval hand holes, E2 repeatedly placed food in one of the two cups and moved the food platform within reach of the subjects until they learned that they could reach through one of the two oval hand holes and retrieve the food reward by opening one of the cups. If the subject chose the cup in which the food was hidden first, it was allowed to retrieve the food. If the subject chose the incorrect cup first, E2 pulled the sliding platform out of reach and showed the subject that the food was in the other cup, but did not give the food to the subject. The food was hidden half the time on the left and half the time on the right.

Introduction. When the subjects knew how to use the apparatus, they were introduced to their informant (E1) who would provide a cue to the location of hidden food in the subsequent test. Half the subjects received the introduction with a competitive informant and half received an introduction with a cooperative informant. The informant sat across the booth and test table from the

Figure 1. The experimental apparatus and the positions of the subjects, social partner (competitive or noncompetitive) and experimenter.

subject so that both were looking directly at each other. As in the warm-up, the session began when the subject was seated or standing in front of the test window. E2 then placed an opaque barrier (70×40 m) between the food platform and the subject, showed the subject that he was holding food, and baited one of the cups with food. Therefore, the subjects knew that food was hidden, but did not know in which cup it was hidden. Then E2 removed the opaque barrier and pushed the food platform within reach of the subject so that it could choose one of the cups. Meanwhile, E1 remained still, while staring at a point slightly above the subject.

Once the subject had chosen one of the cups, E1 behaved in different ways depending on whether they would be a competitive or cooperative informant during the test session.

As a competitor, E1 sat behind a Plexiglas window panel like the subject (except that E1's Plexiglas window had a large hole (10×8 cm) in the centre). This hole allowed E1 to reach his entire forearm out of the window, but not within reach of the food. If the subject chose the correct cup, as it retrieved the food, E1 banged on his Plexiglas window while rocking and staring at the subject. If the subject chose the incorrect cup, E2 immediately slid the food platform within reach of E1 who opened the correct cup and ate the food (occasionally making food grunts) in view of the subject.

As a cooperator, E1 did not sit behind a Plexiglas panel. Instead, the window frame was empty. Therefore, E1 could have reached through the window at any time to grab the hidden food, but did not. If the subject chose the correct cup, E1 loudly encouraged the subject by repeatedly shouting things such as 'good job' in a positive tone and occasionally clapping while the subject retrieved the food. If the subject chose the incorrect cup, E2 immediately slid the food platform within reach of E1 but E2 removed the food and placed it in a food bucket while E1 apologetically shouted phrases such as 'oh, sorry' to the subject.

Test. Immediately after the introduction session, subjects participated in the test session. The procedure of the test session was identical to the introduction except that during the test, once the food was hidden E1 gave a cue to its location.

Reaching cue: if E1 was a competitive informant, once the food was hidden, he reached out of the hole in the Plexiglas window (30 cm) extending effortfully towards the cup where the food was hidden (using his cross lateral arm). The hand was extended palm down and with all fingers extended while the experimenter stared at the correct hiding location.

Pointing cue: if E1 was a cooperative informant, once the food was hidden, he extended his arm (30 cm) and pointed at the correct hiding location (cross lateral arm with only index finger extended) while alternating his gaze between the correct hiding location and the subject.

Design

Half the subjects were introduced and tested with the competitive informant and half with the cooperative informant. The warm-up, introduction and test were given in one session to each subject. Subjects had four to eight trials in the warm-up and another four warm-up trials before and half-way through both the introduction and test. For both the introduction and test sessions subjects had 18 trials. Therefore, they participated in a total of 52 trials in the introduction and test session. Food placement was counterbalanced within a session and across subjects with half the subjects having food hidden in the right cup first and half on the left first. Food was never hidden in the same cup on more than two consecutive trials.

Scoring and analysis

E2 scored live which of the two cups was chosen first by each subject (first cup touched). All trials were videotaped by two video cameras. Each subject's performance in the test session was compared to that expected by chance (within the trials of the test session subjects needed to make 13 correct choices out of 18: binomial probability, one tailed), while the performances of the two groups with the different type of informant were compared to that expected by chance using one-sample t tests and to each other with independent t tests. Finally, we assessed the effects of experience on the subject's performance within test sessions by comparing the number of correct choices within the first nine trials to that in the last nine trials within each group using paired t tests (two tailed).

Results

Table 2 presents the number of correct responses for each of the subjects in the test session. Three of the six subjects who were tested with a human competitor used the reaching cue above chance levels (binomial test: $P<0.05$), but none of the subjects tested with a human cooperator used the pointing cue to find the hidden food. Figure 2 presents the mean number of correct responses for both groups of subjects. As a group, the subjects who were tested with a competitive informant used the reaching cue above chance levels ($t_5 = 3.67$, $P = 0.016$), whereas subjects tested with a cooperative informant did not use the pointing cue at above chance levels ($t_5 = 1.38$, $P = 0.24$). In addition, when the performance of the two groups is compared, the group exposed to a competitor's reaching cue found significantly more food than the group exposed to a cooperator's pointing cue ($t_{10} = 2.82$, $P = 0.018$). Finally, when the first and last halves of the test trials within each group are compared, there was no effect of experience, either when the groups were considered together or separately. Subjects thus came to the experiment with the skills they displayed; they did not learn them in the experiment.

Discussion

Chimpanzees who were introduced to and tested with a human competitor performed better in the object choice task than those who were introduced to and tested with

Table 2. Number of correct choices in the test session by each subject in each experiment

	Experiment							
	1		2		3		4	
Subject	Human reach	Human point	Human compete	Human cooperate	Conspecific reach	Human point	Conspecific compete	Human cooperate
Robert	**13**	—	—	12	9	12	9	9
Riet	12	—	8	—	**15**	9	**15**	9
Jahaga	**17**	—	—	8	**17**	11	12	11
Sandra	**16**	—	11	—	**14**	**16**	11	9
Fifi	11	—	—	10	**15**	14	**15**	11
Trudy	10	—	11	—	**17**	**16**	13	9
Natasha	—	8	—	9	11	9	8	**16**
Fraukje	—	10	7	—	9	9	12	10
Corry	—	9	—	11	11	9	9	9
Ulla	—	11	9	—	10	8	**15**	10
Frodo	—	9	—	9	**16**	15	10	5
Patrick	—	11	9	—	10	9	10	7
Means	**13.17**	9.67	9.17	9.83	**12.83**	11.42	**11.58**	9.67

Scores in bold are significantly above chance level (binomial probability: $P<0.05$).

a human cooperator. It is important to emphasize that during testing, the behavioural and social cues provided by the human were highly similar in the two conditions: the experimenter reached or pointed towards the food with an outstretched arm and hand. What differed across conditions was only the context set up before the test, competitive or cooperative, and the facts that: (1) in the cooperative trials the cooperator alternated his gaze between food location and subject, as is typical in intentional communication (see Tomasello et al. 1985, for observations of gaze alternation in chimpanzees during natural gestural communication); and (2) in the competitive condition the competitor obtained and ate the food reward after trials in which the subject chose

Figure 2. Mean number of correct choices ± SEM by the two groups of subjects tested with either a competitive and cooperative–communicative experimenter in experiment 1. Asterisk indicates that the subjects within a group used the cue provided at above chance level, $P<0.05$. Horizontal line indicates chance level.

incorrectly. In addition, the chimpanzees performed poorly in the cooperative condition even though they had received, in a previous experiment, 50 differentially rewarded trials with a cooperative–communicative experimenter in the object choice task (J. Barth, J. Call & M. Tomasello, unpublished data), and so could have learned the direction of the hand (or some such) as a simple discriminative cue indicating food location.

These results thus provide the first direct support for the competitive cognition hypothesis, in the sense that chimpanzees performed better in the same task under conditions of competition than they did under conditions of cooperation. Further support is provided by informal comparisons of different studies, using different experimental paradigms, in which chimpanzees seem to show their most complex social-cognitive skills in competitive settings, which suggested the hypothesis in the first place (Hare 2001). But precisely how and why competition should activate or facilitate chimpanzees' social-cognitive skills, in a way that cooperation seemingly does not, remains to be determined. As a first step in this direction, in experiment 2 we tested whether the effect observed in experiment 1 is limited to situations in which subjects can exploit the behaviour of others when competing with them, and so use their social-cognitive skills, or whether competing for food improves chimpanzees' performance even in a simple discrimination task in which the individual simply needs to learn that the food is always to be found at the same location (with one shift to the other location in the middle of the trials).

EXPERIMENT 2

Experiment 1 established a basic phenomenon, but the two experimental conditions differed from one another in a number of ways. In a second experiment, therefore, we changed one key parameter: the cognitive task to be
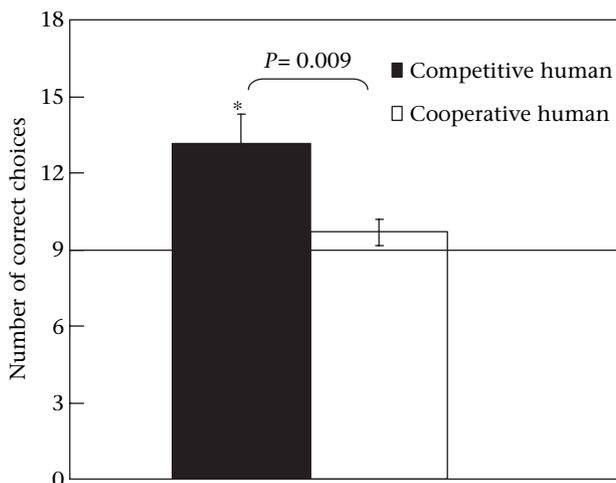
solved (i.e. the nature of the information available for locating the hidden food). In this experiment, subjects had to find hidden food based on where they had seen it hidden in previous trials (it was hidden in the same cup for nine consecutive trials and then in the opposite cup for the last nine trials of a test session) with no social cue given at all. They did this, as in experiment 1, either with a competitive experimenter, who established a competitive relationship before testing and who obtained and ate the food during testing on trials in which the subject was incorrect, or with a noncompetitive experimenter, who established a cooperative relationship before testing and who never obtained or ate the food during testing. The question being asked is thus whether performing in a competitive versus cooperative environment affects chimpanzees' performance in a simple cognitive task in which the competitor and cooperator provide no social cues, and in fact are mainly incidental to the task at hand.

Methods

The subjects and apparatus were the same as in experiment 1 (see Table 2 for the subjects in each test group). The introduction procedure establishing a competitive or cooperative relationship between experimenter and subject, before testing, was also identical. The competitor was the same individual (B.H.) as in experiment 1. The test procedure was also identical except that no cue to the location of the hidden food was provided in either condition (i.e. the experimenter did not reach or point towards the correct cup before the subject made its choice). The only information about the food's location available to subjects during testing was the fact that in the first nine trials the food was hidden in the same cup, and then for the last nine trials of the session it was hidden in the opposite cup. There were two sessions so that subjects had a total of 36 trials (and four warm-ups before each session). Half the subjects in each group had food hidden in the right cup for the first nine trials and in the left cup for the next nine trials, and vice versa for the other group of subjects. Scoring and analysis were the same as in experiment 1. Unless indicated otherwise, all statistical tests were one tailed, because in experiment 1 subjects performed best while competing (this applies to all subsequent experiments).

Results

Table 2 presents the number of correct choices for each of the subjects. No individual in either group found the hidden food at above chance levels (binomial test: NS). Figure 3 presents the mean number of correct responses for both groups of subjects. Neither group found food at above chance levels, and the performance of subjects did not differ between the groups. Finally, when the first nine test trials are compared to the last nine trials within each group there was no evidence for learning overall, although subjects found significantly less food in the last nine trials than in their first nine trials with a noncompetitive experimenter ($t_5 = 6.51$, $P = 0.002$). All but one subject
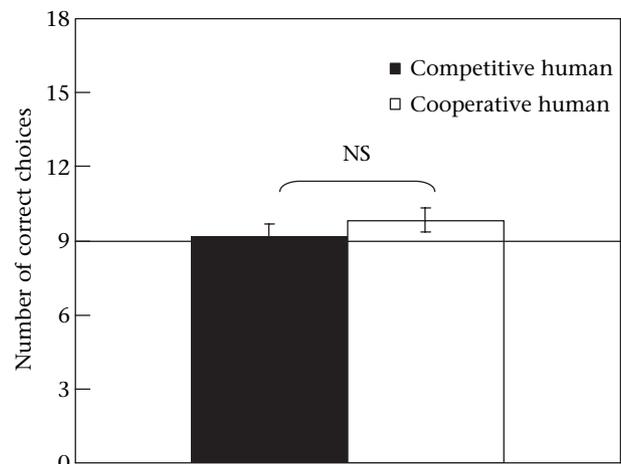

Figure 3. Mean number of correct choices $\pm$ SEM by the two groups of subjects tested with either a competitive or a non-competitive human in experiment 2. Horizontal line indicates chance level.

had a significant preference (14 or more trials; binomial test two tailed: $P < 0.05$) for choosing only one of the two cups throughout the test session.

Discussion

The competitive context did not make a difference to chimpanzees' performance in this simple discrimination task in which the location of hidden food was best predicted by its location on the previous trial. In this task, the cooperator and competitor were essentially nothing more than onlookers, unlike in experiment 1 where they gave the essential cue to the food's location. One interpretation of this result is that the kind of cue provided in experiment 1 was a crucial part of the experimental manipulation. Specifically, it may be that subjects perceived the reaching as one instance of trying to accomplish something, since in other studies chimpanzees have shown the ability to distinguish trying from not trying (Call et al., in press). On the other hand, they did not know what to make of the pointing gesture, which did not look like trying because the human's reach was not blocked and she alternated her gaze (whereas in trying the human stays focused on the goal).

Alternatively, it is possible that this task was simply too difficult, given that no individual or group found food at above chance levels. In the object choice tasks in which these same subjects have previously been tested (J. Barth, J. Call & M. Tomasello, unpublished data), food was not hidden in the same hiding location for more than two trials in a row (including in the introduction of the current experiment). When subjects cannot find food reliably, they frequently develop an optimizing strategy in which they exclusively choose the same cup (Itakura et al. 1999). By repeatedly choosing the same cup they are assured of (1) going no more than two trials without finding food and (2) finding food in half the trials (assuming side is counterbalanced). Indeed, an examination

of subject errors shows that all but one subject had a significant side bias for one cup. This suggests that in this first exposure to the new baiting regime, subjects were overly committed to their optimizing strategy regardless of their social partner, given that they did not find the information provided very salient.

Finally, it was only when subjects were tested with a noncompetitive human that they found significantly less food in their last nine trials than in their first nine trials. While only suggestive, subjects may have maintained their level of performance because they were more motivated when competing. If true, perhaps subjects will be even more motivated and find more food if they are tested on the same task again, but this time with a conspecific competitor replacing the human competitor. To test the effect of a conspecific competitor on the performance of subjects, we again tested subjects using the same two cognitive tasks in experiments 1 and 2, except that a conspecific competitor was substituted for the human competitor.

EXPERIMENT 3

Experiment 3 was a replication of experiment 1 with the exception that the competitive informant in this task was a conspecific. In addition, unlike the first two experiments all subjects were tested with this conspecific first. It was only after all subjects had competed against a conspecific that they were again tested with a cooperative–communicative human informant. Our prediction was that even though all subjects would have more exposure to the social cue being provided (extended arm and hand) when tested with a cooperative human, they would still find less food than they did when previously tested with a competitive conspecific who provided the same cue.

Methods

Subjects

Subjects were the same as in experiments 1 and 2. Two of the 12 subjects played the role of competitor in place of E1 (competitive informant). These conspecific competitive informants were chosen based on their size, motivation and rank within the group. After experiment 2 was

completed and before the current experiment, 11 of our subjects (Ulla was not tested) participated in Hare et al.'s (2002) study, in which a cooperative–communicative human indicated the location of hidden food to subjects by gazing at, reaching towards, touching and leaving a wooden block on top of the baited cup. Only two (Trudy and Patrick) of the 11 subjects tested used these conspicuous social cues to find the hidden food at above chance levels (meanwhile nine of 11 dogs used the same cues to find the hidden food). Note that all three subjects who used the cues of the competitor in experiment 1 again failed to use a similar cue when it was provided by a cooperative–communicative human informant.

Apparatus

Again, a table was placed in the test booth between two Plexiglas test windows. A few modifications were made to the table and the Plexiglas window on the side of the informant to make it possible to have either a conspecific or a human informant (Fig. 4). For both informants the window frame was partially occluded by pieces of opaque plastic (60×25 cm) so the subject could see the informant only when its body and head were equidistant between the two cups. In addition, when a conspecific was the informant an additional piece of plastic could be placed over the hole (10×8 cm) in its Plexiglas window that created a smaller vertical oval (7×3 cm). Finally, a piece of Plexiglas (65×10 cm) was attached on the subject's side of the food platform via a metal slide (allowing it to slide 14 cm). Therefore, to choose and open one of the two cups on the food platform, subjects first needed to push the Plexiglas out of the way.

Procedure

Before testing, a conspecific informant was identified that would reliably reach out towards a cup of food when placed just out of reach on the food platform while another chimpanzee was across the table. Food (half a banana) was placed on the food platform and once both subjects were at the test window the food platform was moved towards the conspecific informant until the food was just out of reach. The informant (Trudy) was tested dyadically (six pilot trials) with the most dominant female (Riet) and she reliably reached for the out-of-reach food
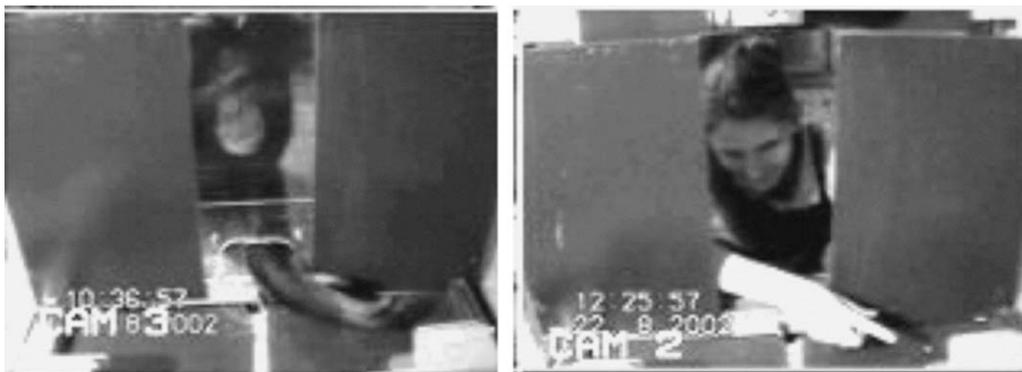

Figure 4. The social cue provided by the competitive conspecific and the noncompetitive human in experiment 3.

(Patrick was Trudy's informant). Once the informant was identified, all the subjects were briefly (4–8 trials) reintroduced to the apparatus to make sure that they were acquainted with the modifications to the apparatus. The subjects were shown that food they had seen hidden could be retrieved by (1) sliding the Plexiglas attached to the food platform to one side and (2) pushing open one of the two cups (attached with hinges to the sliding food platform).

Introduction. As in the first two studies, the subjects were introduced to their informant before the test session. After the subject approached the test window and the informant was ready, an opaque occluder (1×0.5 m) was placed in front of the informant's window so she was not visible to the subject. Then an opaque occluder (70×40 cm) was positioned between the food containers and the subject while food was hidden in one of the two cups. Therefore, subjects knew that food was hidden but did not know in which cup it was hidden. Once the food was hidden, E2 removed the opaque occluder hiding the cups, pushed the food platform towards the subject, and allowed it to reach through one of the choice holes. If the subject chose the correct cup, it was allowed to retrieve the food and (1) the human informant loudly praised the subject or (2) the conspecific competitor often showed signs of frustration (screaming, shaking hands vigorously, rocking, or pacing). If the subject chose the incorrect cup, the occluder in front of the informant was removed, the food platform was moved out of reach and (1) E2 removed the food while E1 said 'so sorry!' or (2) the conspecific competitor was allowed to retrieve the food.

Test. The procedure was the same as that in the introduction with the exception that (1) an opaque barrier was not placed in front of the informants so that they could watch the baiting, (2) once the food was hidden the food platform was first pushed in the direction of the informant so that she could provide a cue to the food location (Fig. 4) and (3) during all test sessions a number of motivational trials were included in which the food was hidden, as in a test trial, but the conspecific competitor was allowed to retrieve the hidden food while E2 retrieved the food from the cups once it was pushed towards the cooperative–communicative human.

Design

All subjects were tested with the conspecific informant first and the human informant second. In each introduction and test, subjects had four warm-up trials and 18 test trials. In addition, within the test session nine motivational trials were conducted (to maintain the informant's motivation for reaching). Therefore, subjects participated in a total of 53 trials. Food placement was counterbalanced within sessions and across subjects with half the subjects having food hidden in the right cup first and half on the left first. Food was never hidden in the same cup on more than two consecutive trials. Scoring was the same as in the previous experiments.

Results

Table 2 presents the number of correct responses for each of the subjects in the test session. Six of 12 subjects who were tested with a conspecific competitor used the reaching cue above chance levels to find the hidden food; four of 12 subjects tested with the human informant used the pointing cue to find the hidden food (binomial test: $P<0.05$). Figure 5 presents the mean number of correct responses for both groups of subjects. As a group, the subjects found the food at above chance levels when cued by a conspecific competitor and a human informant (conspecific competitor: $t_{11} = 4.24$, $P<0.001$; human informant: $t_{11} = 2.74$, $P = 0.02$). However, when the two groups are directly compared, subjects found significantly more food when they were competing against a conspecific competitor than when they were cooperating with a human ($t_{11} = 1.85$, $P = 0.045$). Finally, when the first nine trials are compared to the last nine trials in each session there was no effect of experience.

Discussion

As in experiment 1, chimpanzees in experiment 3 were more successful at using a social cue to find hidden food when they were competing than when they were cooperating. The difference was that in this case the other individual against which they were competing was a conspecific (the cooperator, of course, had to be a human again). This was true even though subjects had less experience when tested with the competitor (all subjects were tested with a conspecific competitor first). However, subjects were better in the cooperation condition of this study than they were in experiment 1, even though the conditions were basically identical. The most plausible explanation is that chimpanzees can learn to exploit a pointing cue with some experience, as established by previous research (Povinelli et al. 1997; Call et al. 1998, 2000), and so by the time they engaged in this condition they had learned to use arm extension as a discriminative cue to the food's location. Evidence for this interpretation
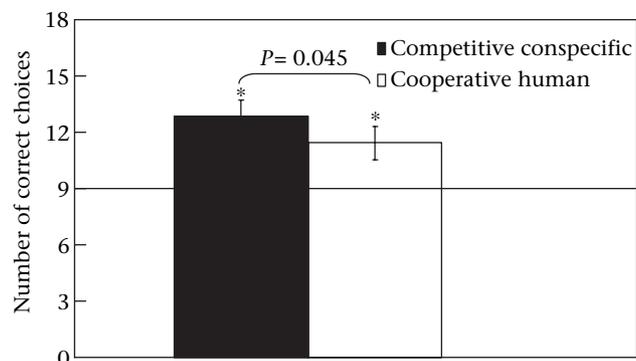
Figure 5. Mean number of correct choices ± SEM by subjects when tested with either a competitive conspecific or a cooperative–communicative human in experiment 3. Asterisk indicates that the subjects within a group used the cue provided at above chance level, $P<0.05$. Horizontal line indicates chance level.

is the fact that all of the individuals who used the cues of a cooperative−communicative human successfully in this experiment had already been successful using the social cue when competing either in experiment 1 or in the first session of this experiment.
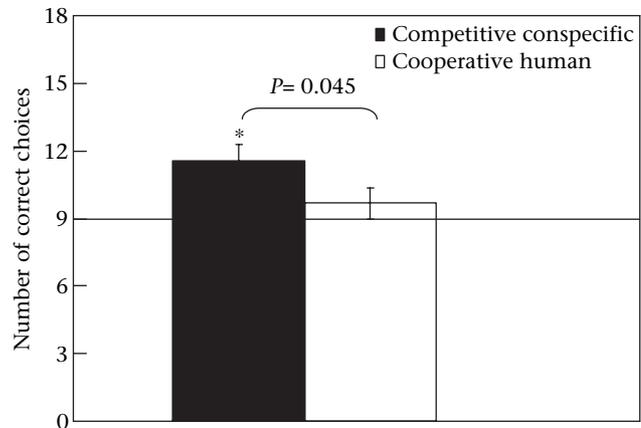
EXPERIMENT 4

Experiment 4 was a replication of experiment 2 (discrimination location task), with the exception that the competitive informant in this task was a conspecific. In addition, like experiment 3 using a conspecific competitor, it was only after all subjects had competed against the conspecific that they were again tested with a noncompetitive human. Although in experiment 2 subjects did not find more food in this simple task when competing against a human, we predicted that they would perform more skilfully in this experiment when they were competing against a groupmate with whom they competed on a daily basis.

Methods

The subjects and apparatus were the same as in experiment 3 (conspecific competitor). The procedure was basically the same as in experiment 2 (discrimination location task). The subjects (as well as the conspecific competitors) had four warm-up trials and 18 introduction trials in which food was hidden in one of the two cups for no more than two consecutive trials and placement was counterbalanced within and between subjects. After the introduction, subjects again received four warm-up trials (as did the conspecific competitor), and then in the test session food was hidden in one of the cups for blocks of nine trials (the placement on the first trial was counterbalanced across subjects). Therefore, subjects received a total of 44 trials. Scoring and analysis were the same as in the previous experiments. One small difference in procedure is that in this experiment the conspecific's/human's Plexiglas window was covered throughout the trial (in both the introduction and test) until the subject chose to search one of the cups (therefore informants provided no social cues at the time of choice).

Results

Table 2 presents the number of correct responses for each of the subjects in each condition. Four of 12 subjects who were tested with a competitive conspecific found the food at above chance levels; only one of 12 subjects found the hidden food at above chance levels when tested with the noncompetitive human (binomial test: $P < 0.05$). Figure 6 presents the mean number of correct responses for both conditions. As a group, subjects found food at above chance levels when competing against a conspecific ($t_{11} = 3.58$, $P = 0.002$), but not with the noncompetitive human ($t_{11} = 0.86$, $P = 0.394$). In addition, subjects found significantly more food when competing against a conspecific than when interacting with a noncompetitive

Figure 6. Mean number of correct choices $\pm$ SEM by subjects when tested with either a competitive conspecific or a noncompetitive human in experiment 4. Asterisk indicates that the subjects within a group used the cue provided at above chance level, $P < 0.05$. Horizontal line indicates chance level.

human ($t_{11} = 1.86$, $P = 0.044$). Finally, when the first nine trials are compared to the last nine trials in both test sessions, there was no effect of experience within either session.

Discussion

In experiment 2, chimpanzees did not learn reliably to find food in the location they last found it regardless of whether they were paired with a cooperative or a competitive human. In this experiment, they finally learned to do this, but only when competing against a conspecific (not in the presence of a noncompetitive human). Again, as in experiment 3, this difference was found even though subjects had more experience with this task when they were tested with a noncompetitive human than when they were tested with a competitive conspecific. Because the information available to subjects in the two conditions of this experiment was identical, the most likely explanation for the results is that subjects were simply more motivated when competing. The results of this experiment thus suggest that chimpanzees are more skilled at finding food when competing across a wide range of tasks. The negative results of experiment 2 are probably the result of the difficulty of the task; it took them many trials to learn it, and they learned it first only in experiment 4. They did this only with the conspecific competitor; whether they would have learned it just as well with a human competitor in experiment 4 is an open question.

GENERAL DISCUSSION

Chimpanzees performed better in two different tasks when competing than when cooperating. In the standard object choice task, this finding was robust regardless of whether the competitor was a human or another chimpanzee. In a simple discrimination location task in which

food was repeatedly found at the same location (with one switch), chimpanzees did not at first become skilful whether competing or cooperating with a human; they later became skilful, but only when competing (not co-operating) with a conspecific. Although comparison with other studies had suggested that chimpanzees display their most sophisticated cognitive skills in competition rather than in cooperation, this is the first study to demonstrate this directly in a single experimental paradigm.

Experiments 1 and 3 were designed to replicate the standard object choice procedure that has become increasingly popular in testing the ability of animals to exploit the social cues of others. Most research with chimpanzees using the object choice paradigm has found that subjects typically require considerable experience before they reliably use human social cues to find hidden food. Experiments 1 and 3 demonstrate that it is possible to improve subjects' spontaneous performance with social cues in this same task by simply having them compete. Critically, in both experiments what varied between the types of interactants was not the available social cue, an outstretched arm and hand in both cases, but instead the social context in which the cue was provided. The context was differentiated by introducing the subjects to two types of interactants who reacted to their success and failure in opposite ways. While the competitor protested the subjects' success and ate the reward when they were wrong, the cooperative communicator was supportive of the subject in success and failure and never ate the food reward. It was only after subjects were introduced to their social partner that the competitor unintentionally informed the subject as they reached for the out-of-reach food, whereas the cooperative communicator intentionally communicated to the subject by pointing to the food within his reach. In support of the competitive cognition hypothesis, the main finding was that subjects found more food when their partner was a competitor. Therefore, from these results it seems that chimpanzees may be more skilled or motivated to exploit social cues when they are competing over the food rewards.

Experiments 2 and 4 found that this effect is not confined to the object choice task involving the reading of a social cue at the time of choice, but it also extended to a simple discrimination task in which there were no social cues. In these experiments subjects were again introduced and tested either with a competitive or a noncompetitive social partner, but in a task where food location on the previous trial was the only cue. Specifically, subjects could reliably find the food only by remembering where they had either found or seen food hidden at the end of the previous trial. In experiment 2 subjects were unsuccessful regardless of the social context. However, in experiment 4 subjects found more food when they were competing against a conspecific than when they were interacting with a noncompetitive human. This suggests that the competitive cognition hypothesis applies to a range of cognitive tasks. Because experiment 2 was run before experiment 4, it is not totally clear if the conspecific competitor is a crucial part of the competition effect in this task.

The findings of experiments 1 and 3 are consistent with the hypothesis that chimpanzees do not understand the communicative intentions of humans. The critical test for this hypothesis is each subject's first encounter with the pointing cue before it can simply learn a contingency between the cue and the food location. In the first experiment, six subjects were given the pointing cue by a human who had demonstrated no interest in the food reward during the introduction. All of these subjects were unable to find the food with the pointing cue. Subsequently in experiment 3, only subjects who had previously been successful using a competitor's reaching cue were also successful when in their next session a human pointed. Perhaps most striking are the performances of two subjects, Riet and Jahaga, who were both successful using the cues of a competitor, but then were unable to use the same social cue to find food when the cue was provided by a cooperative–communicative human. Conversely, no subject was able to use the social cue of a cooperative–communicative human but not that of a competitor. Therefore, these results support the hypothesis that chimpanzees do not understand the communicative intent of a cooperative–communicative experimenter.

However, at the same time that the results of experiments 1 and 3 support the communicative intent hypothesis they are also consistent with a motivational hypothesis. Subjects may have found more hidden food when competing in these experiments because they were more motivated to succeed and paid more attention when competing. The strongest evidence for this hypothesis comes from experiments 2 and 4 where subjects could not base their decision on an available social cue at the time of choice. Subjects were successful at finding hidden food only when competing against a conspecific, arguably the most motivating social partner given that this competitor was an individual with whom subjects competed daily. However, this explanation must account for the subjects' success in experiment 1 and failure in experiment 2 with a human competitor. One plausible explanation is that the task used in experiments 2 and 4 was simply more difficult given that there were no cues to the food's location at the time of choice. Therefore, success in this uncued task required a more motivating social partner, a conspecific competitor. Alternatively, subjects' performances in experiments 2 and 4 may be the result not of differences in motivational levels, but of learning. For example, subjects may have performed better in experiment 4 because they had the benefit of participating in experiment 2. However, this learning hypothesis cannot be the only factor explaining the subjects' performance in experiment 4, since they fell back to chance levels when tested with a noncompetitive human. Therefore, if there was learning, it was specific to the competitive social context.

Although there may be various ways to explain the effect of competition on chimpanzees' performance in cognitive tasks, our study has shown with quantitative comparisons that there is a phenomenon that needs explanation. This phenomenon highlights the importance of an ecological approach to theories of cognitive

evolution and to the design of cognitive experiments. There are few experiments designed specifically to investigate the socioecology of primate social cognition (but see Drea & Wallen 1999, for an exception), and there are no agreed-upon conventions for how to maximize the ecological validity of cognitive tasks for use with chimpanzees (e.g. would being tested in a social group make a difference and should males and females be tested in the same way?). Cognitive skills evolve to solve ecological problems relevant to maximizing survival and reproduction, and so to understand the process of cognitive evolution in any species we must identify the types of ecological problems that have driven their cognitive evolution. We must also attempt to understand how cognitive skills are integrated with and possibly constrained by other psychological systems (e.g. emotional/motivational) that have also evolved to maximize survival and reproduction.

Acknowledgments

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