Chimpanzees know what conspecifics do and do not see

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We report a series of experiments on social problem solving in chimpanzees, *Pan troglodytes*. In each experiment a subordinate and a dominant individual were put into competition over two pieces of food. In all experiments dominants obtained virtually all of the foods to which they had good visual and physical access. However, subordinates were successful quite often in three situations in which they had better visual access to the food than the dominant, for example, when the food was positioned so that only the subordinate (and not the dominant) could see it. In some cases, the subordinate might have been monitoring the behaviour of the dominant directly and simply avoided the food that the dominant was moving towards (which just happened to be the one it could see). In other cases, however, we ruled out this possibility by giving subordinates a small headstart and forcing them to make their choice (to go to the food that both competitors could see, or the food that only they could see) before the dominant was released into the area. Together with other recent studies, the present investigation suggests that chimpanzees know what conspecifics can and cannot see, and, furthermore, that they use this knowledge to devise effective social-cognitive strategies in naturally occurring food competition situations.

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A central question in the study of primate cognition is what individuals know about the psychological processes of other individuals. Initially, for theoretical reasons, most of the research focused on what nonhuman primates know about various 'high-level' psychological processes, such as the beliefs and intentions of others. Unfortunately, this research has come to no clear consensus (see Tomasello & Call 1994, 1997; Heyes 1998 for reviews). Although some researchers contend that observations of apparently deceptive behaviours in the wild are good evidence of this kind of social cognition (e.g. Byrne 1995), others point to experiments that, in general, have found either negative results (Povinelli et al. 1994, 1998; Call & Tomasello 1999) or positive results only after many trials in which learning could have taken place (Premack & Woodruff 1978; Woodruff & Premack 1979; Povinelli et al. 1990; but cf. Call & Tomasello 1998). This research has also suffered from the difficulties of operationalizing elusive psychological phenomena such as beliefs and intentions.

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Recently, however, a number of studies have focused on what nonhuman primates know about the relatively 'low-level' psychological process of visual perception, a process that, initially at least, is much easier to operationalize behaviourally than many of the so-called higher-level processes. The question is simply what individuals know about the visual experience of other individuals: do they know that others see things and that this affects their behaviour in predictable ways? This understanding may take different forms, from an individual's use of the gaze direction of others as a behavioural cue to the understanding that the visual experience of others is analogous to one's own visual experience. Differences in this kind of social/psychological understanding might have significant effects on the way in which different species or individuals are able to find food, avoid predators, and monitor and predict the social interactions of groupmates.

There is now solid experimental evidence that many nonhuman primate species, especially chimpanzees, *Pan troglodytes*, reliably follow the gaze direction of conspecifics to external targets. For example, Tomasello et al. (1998) found that five different species (*P. troglodytes*, *Cercocebus torquatus* and three species of *Macaca*) reliably followed the experimentally induced gaze direction of a conspecific (see also Emery et al. 1997). One explanation for this behaviour is simply that individuals learn,

through experience, that when they look in the direction towards which another individual is visually oriented, they often find something interesting or important. The cognitive process might thus be: turn in the direction in which others are oriented and then search randomly until you find something interesting. However, after a suggestive finding of Povinelli & Eddy (1996a), Tomasello et al. (1999) established that chimpanzees do not just look in the direction of others and search randomly, but they track geometrically the gaze direction of others to specific targets, looking around barriers and past distractors in the process. Call et al. (1998) also found that when a chimpanzee tracked the gaze of another individual to a location and found nothing interesting there, it often looked back to the individual's face and tracked its gaze direction a second time: 'checking back' in this way is a much-used criterion in assessing human infants' understanding of the visual experience of others (Bates 1979).

The problem is that there are also studies in which chimpanzees do not seem to show a deep understanding of the visual behaviour of others. There are two sets of studies, both of which require individuals not just to track the gaze direction of others, but to base a foraging decision on the visual behaviour or experience of another individual (typically but not always a human). First, Povinelli & Eddy (1996b) presented chimpanzees with two human experimenters from whom they could potentially beg food. One could see them and their begging gesture, while the other, for various reasons (including having a bucket over his head), could not. The chimpanzees were insensitive to all but the most obvious cues; that is, they tended to beg indiscriminately from both the human who could and the human who could not see them and their gesture (see also Call & Tomasello 1994).

Second, chimpanzees have shown very little ability and/or inclination to use the gaze direction of others to locate hidden food. Call et al. (1998) presented chimpanzees with two opaque containers, only one of which contained food (with chimpanzees trained to know that they could choose only one). A human experimenter then looked continuously at the container with food inside. Not one of six chimpanzees used this cue to find the food. (Tomasello et al. 1997 provided chimpanzees with three different visual-gestural cues in this same paradigm and also found negative results.) Povinelli & Eddy (1996c) found that some young chimpanzees could learn to use gaze direction cues in a similar experimental situation, but they also showed that this was only a learned behavioural cue, not an indicator of the visual experience of others (e.g. turning the head in the correct direction but looking to the ceiling was just as effective as staring at the correct container). Itakura et al. (in press) used a trained chimpanzee conspecific to give the gaze direction cue (the rear of one of the opaque containers was left open so that the trained conspecific simply looked at the food while staying physically equidistant between them), but still found mostly negative results (i.e. no use of conspecific gaze cue); their only positive result was that chimpanzees did find the food if the cue giver (either chimpanzee or human) approached the correct container and inspected it, as if foraging for food.

It is unclear why chimpanzees who follow the gaze direction of others so naturally in some situations have so much trouble in using the gaze direction of others when they are attempting to obtain or find food. One explanation is that these situations are very unusual for chimpanzees (and other nonhuman primates). They are accustomed to competing for food, and indeed it is unlikely that they have ever experienced in their natural social lives a conspecific attempting to help them find food (when that conspecific could keep it for itself). Evolutionarily, it is competition for food, and not sharing information about monopolizable food resources, that characterizes primate social life (Wrangham 1980; Hauser et al. 1993). Moreover, each of these experiments also had some 'arbitrary' rules not involving an understanding of visual experience (e.g. that there can be only one choice per trial). It is thus possible that in other, more natural competitive situations, chimpanzees may show more skill in understanding that the gaze direction of others can be used to make maximally effective foraging decisions.

We therefore attempted to design a relatively natural social situation in which one chimpanzee, a subordinate, competed for food with one of its groupmates, a dominant. In each case, the subordinate had to choose between one of two pieces of food and could maximize the effectiveness of that choice by taking into account its dominant competitor's visual access, or lack of visual access, to each of those pieces of food. No training was required to prepare the individuals for this competitive situation, no human intervention was required at any point (other than setting up the trials) and no special rules of the competition had to be learned. When the use of other behavioural cues is systematically ruled out, these experiments have the potential to provide more naturalistic, and yet still reliable, evidence about whether chimpanzees know what conspecifics do and do not see.

PILOT EXPERIMENT

We first established the dominance relationships among pairs of chimpanzees for use in the main experiments (i.e. dominance only in the sense of pairwise dominance in competition for food) and then evaluated a method for inducing food competition between pairs of chimpanzees. The main focus in all studies was on the behaviour of subordinate individuals.

Methods

Subjects

Ten adult and subadult chimpanzees (mean age 20.44 years) housed in two social groups at the Yerkes Regional Primate Research Center Field Station participated in this study (see Table 1). Seven of the 10 chimpanzees were subordinate to someone else in their group and contributed to the data set, whereas the other three (Peony, Tai and Ericka) were all high-ranking individuals in their respective groups and so were used only to obtain data on the seven subordinate subjects. All chimpanzees were

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 experiments	Rearing history	Dominance rank
Group 1						
Peony	30	Female	Wild	Pilot, 1–5	Nursery–home	1
Borie	34	Female	Wild	Pilot, 1–5	Mother	2
Rita	11	Female	Captivity	Pilot, 1–5	Mother	3
Anja	18	Female	Captivity	Pilot, 1–5	Mother	4
Rennette	11	Female	Captivity	Pilot, 1–5	Mother	5
Kate	9	Female	Captivity	1–4	Mother	6
Donna	8	Female	Captivity	Pilot, 1–5	Mother	7
Group 2						
Ericka	25	Female	Captivity	Pilot	Home	1
Tai	31	Female	Wild	Pilot, 1–5	Mother	1
Phineas	32	Male	Wild	1–5	Mother	2
Cynthia	18	Female	Captivity	Pilot, 1–5	Nursery	3
Magnum	9	Male	Captivity	Pilot, 1–5	Nursery	4

captive born except Peony and Tai who were wild born. All subjects were housed in a set of five indoor cages ($3 \times 3 \times 3$ m) and an outdoor compound (24×30 m) which contained climbing structures and various objects such as balls, barrels, logs and tyres. They were fed twice daily on a diet of fruit, vegetables and chow, as was their normal routine. Water was available ad libitum and subjects were not food deprived at any time.

Procedure

Subjects were tested in their indoor cages (ca. 27 m^3 each), which consisted of five adjacent cages in a single row with a single service hallway. In each cage, three of the cage walls and the floor were made of concrete; the cage ceiling and the wall facing the service hallway were made of wire mesh. The wall separating adjacent cages protruded ca. 50 cm into the hallway, making it impossible to see from inside one cage into an adjoining cage except through the connecting doorway when it was opened. (This small protruding wall was also used to help experimenters hide their actions from subjects.) The majority of cages had three doors (0.6 m^2); two gave access to adjacent indoor cages to the left and right, while the third gave access to the outdoor enclosure (closed at all times for these experiments). The floor was bare and cages had some elevated platforms where subjects could sit or lie down.

Subjects were tested in pairs consisting of one dominant and one subordinate animal. Before testing began, we conducted preliminary tests of dominance using a food competition test. We introduced a single pair of animals into the same cage and placed a piece of fruit inside the cage approximately equidistant between them. Subjects who obtained the food in the presence of others were deemed dominant over them. This test was repeated twice. Table 1 shows the results of the food dominance tests (which were further confirmed in this study). Once the food-competition dominance hierarchy was established, testing began.

For testing, a dominant and a subordinate individual were housed in two adjacent cages. The door connecting the cages was open at all times, so that subjects could move freely between them. Before starting a trial, the human experimenter (E1) waited until subjects occupied a set of predetermined positions (see below), sometimes encouraging them to these positions by dropping small pieces of fruit on that location. Once subjects reached these predetermined positions, another human experimenter (E2) dropped the target food (a whole banana, much larger than the pieces used to position subjects) at another predetermined location. There were four types of test as defined by the location of the subjects and the location of the target food.

(1) Subjects centred, food in subordinate's cage. The two individuals were positioned in the centre of their respective cages so that they could see one another through the open door. E2 then surreptitiously introduced the target food into the subordinate's cage immediately next to the wall separating the cages, with the hiding process occluded from the dominant individual by the small protruding wall.

(2) Subjects centred in dominant's cage, food in dominant's cage. The two individuals were positioned so that they were both in the dominant's cage. The target food was then introduced approximately equidistant between them (a kind of replication of the original dominance testing).

(3) Subordinate in door, food in subordinate's cage. The subordinate individual was positioned inside the doorway connecting the cages and the dominant was in its cage. E2 then surreptitiously introduced the target food into the subordinate's cage against the wall separating the two cages.

(4) Subordinate in door, food in dominant's cage. The subordinate individual was positioned inside the doorway connecting the cages and the dominant was in its cage. E2 then introduced the target food next to the wall in the dominant's cage, approximately equidistant

between the two animals (another replication of the dominance testing).

All possible pairs of subordinate–dominant animals in both groups were tested (except that Ericka and Tai from group 2 were not tested as a pair because they were equally dominant). This meant that some individuals were tested more than once in the experimental conditions (up to four times) because they had several other individuals dominant to them, whereas other individuals (e.g. second ranking) were tested only once. Owing to the exploratory nature of this experiment, individual pairs were given multiple trials in each condition, and this often differed across pairs.

Scoring and data analysis

In each trial E1 and E2 jointly determined and recorded who obtained the food. This determination was straightforward and unambiguous in every case (and this was true in all of the subsequent experiments as well), and so reliability assessments were deemed unnecessary. Analyses in all cases focused on the subordinate individual, and each of these individuals received only one score for a given condition no matter how many trials it had. To do this, we converted the scores of all individuals to 'percentage success' scores. For example, a given subject might be paired with three different dominant animals on three different trials in the same condition; if it obtained the target food once, its score for that condition was 33%. We followed this procedure to generate one number for each subject for each condition.

Results

The four conditions may be seen as two pairs. For one pair of conditions, subjects were positioned in the centre of their cages (food was then introduced into either the dominant's or subordinate's cage), and in the second pair the subordinate animal was positioned in the doorway (food was then introduced into either the dominant's or subordinate's cage). The results are straightforward. In the pair of conditions in which subjects were centred in their cages, subordinates obtained a significantly greater percentage of food when it was introduced into their cage (ca. 20 times as much) than when it was introduced into the dominant's cage (Wilcoxon test: $T=15$, $N=5$, $P=0.05$). Similarly, in the pair in which the subordinate was in the doorway, subordinates again obtained a significantly greater percentage of food when it was introduced into their cage than when it was introduced into the dominant's cage (Wilcoxon test: $T=21$, $N=6$, $P<0.05$), by an order of magnitude of about 10 times.

Discussion

This pilot experiment established two facts important for the main experiments. First, the dominance rankings were essentially replicated three times. In the two experimental conditions in which both animals had equal visual and physical access to the food, the individuals that had previously been designated as dominant obtained the food almost all of the time in both conditions. Second, the method was found to be a fair one for testing food competition in that subordinates could obtain the food quite reliably in certain circumstances. That is, in the experimental conditions in which the food was more readily accessible to the subordinates than to their dominant rivals, both visually and physically, they obtained the food almost all of the time.

EXPERIMENT 1: THE WALL TEST

The pilot experiment gave subordinate individuals a huge competitive advantage in the two conditions in which the dominant did not know food was available. In these conditions the subordinate could simply walk over to the food and take it without any reaction from the dominant, since the dominant was absent from the room. In experiment 1 the situation was more challenging. In all trials there were two target foods available, with at least one always in plain sight of both individuals (and equidistant to them) in the open doorway. This meant that at some point in the trial the dominant always approached the subordinate's cage. The interesting variation was that the second target food was available at different places, for example sometimes in the subordinate's cage, out of the dominant's sight, in different experimental conditions. We predicted that subordinate animals would preferentially target the food hidden from the dominant's view.

Methods

Subjects

Eleven adult and subadult chimpanzees participated in this study (mean age 19.2; see Table 1). Nine of those 11 chimpanzees were subordinate to someone else in their group and contributed to the data set whereas the other two (both dominant in their respective groups) were used only to obtain data on the nine subordinate subjects.

Procedure

We used the same general methodology as in the pilot experiment. Pairs of dominant and subordinate animals were housed in four adjacent cages (see Fig. 1). At the beginning of each trial, each subject was confined to one of the extreme cages (cages 1 and 4, Fig. 1) while E1 introduced two pieces of fruit (half-bananas) inside the middle cages (cages 2 and 3, Fig. 1). At the start of each trial, the doors connecting cages 1 and 2 and cages 3 and 4 were completely closed so that subjects were unable to witness the baiting process. The door connecting cages 2 and 3 remained open throughout the experiment. To begin, E1 entered the middle cages and deposited two pieces of fruit in one of three predetermined configurations corresponding to the three test conditions (subjects could not see this). Test conditions varied as a function of the placement of the fruit, and this determined who could and could not see one of the pieces of fruit when the doors were opened.

(1) Dominant–Door. One piece of fruit was in the doorway (equally accessible visually and physically to
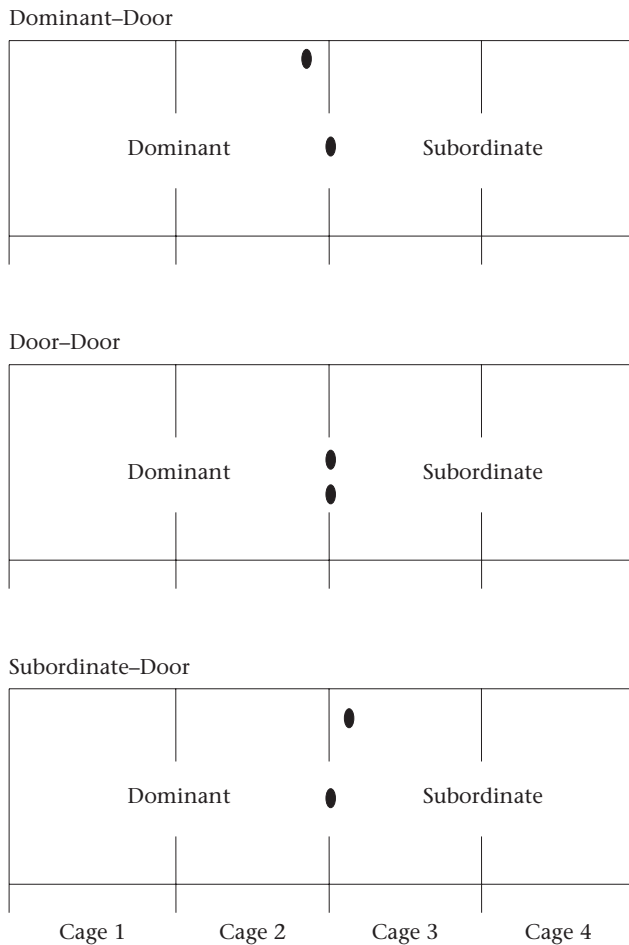
Dominant–Door

Door–Door

Subordinate–Door

Cage 1   Cage 2   Cage 3   Cage 4

Figure 1. Experimental conditions in the wall test (experiment 1).

both subjects), whereas the other piece was in the dominant's cage next to the wall separating cages 2 and 3 (visually and physically blocked from the subordinate), ca. 50 cm from the piece in the doorway.

(2) Door–Door. Both pieces of fruit were placed on the door ledge between cages 2 and 3, separated by ca. 50 cm. The two pieces of fruit were thus equally visible and equally accessible physically to the two subjects.

(3) Subordinate–Door. One piece of fruit was in the doorway (equally accessible visually and physically to both subjects), whereas the other piece was in the subordinate's cage next to the wall separating cages 2 and 3 (visually and physically blocked from the dominant), ca. 50 cm away from the piece in the doorway.

After completing the baiting process in one of these ways, E left the cages and two other experimenters simultaneously raised each of the closed doors 15 cm. This opening permitted subjects to look into the adjacent cage and through the open door to the position of their test mates, but it did not allow them to enter the middle cages. After about 5 s, when both subjects had looked through their respective doors, both doors were simultaneously raised releasing the subjects into the middle cages.

All possible pairs of subordinate-dominant animals in both groups were tested twice in each condition (27 pairs × 3 conditions × 2 trials=162 total trials). Each pair of subjects was run in each of the trials in each of the three conditions one after the other, typically with one condition per day and no more than a few days between conditions. Across subjects, order of conditions was counterbalanced.

Scoring and data analysis

As in the pilot experiment, in each trial E1 and E2 recorded who obtained the food, a straightforward determination, and the order in which they did so. As in the pilot experiment, the nine subordinate animals were the focus of study. In some cases, they were paired with multiple dominant individuals, and so again we used percentages to obtain one score per individual per experimental condition. All statistical tests were one-tailed unless otherwise indicated.

Results

Figure 2a shows the percentage of pieces obtained by subordinate subjects in each of the three test conditions. Overall, there were significant differences between conditions (Friedman test: χ^2_2=12.72, N=9, P<0.001). Pairwise comparisons between conditions indicated that subjects obtained a significantly larger percentage of pieces in the Subordinate–Door condition than in the Dominant–Door (Wilcoxon test: T=45, N=9, P<0.01) and the Door–Door (Wilcoxon test: T=36, N=8, P<0.01) conditions. There were no significant differences between the percentages of pieces subordinate animals obtained in the Dominant–Door and the Door–Door conditions.

Also important was which piece of food the subordinate obtained when it did obtain food. Figure 2b shows the percentage of pieces obtained by subordinates in each condition as a function of whether the food was visible or hidden to them and their partners. In the Subordinate–Door condition, subordinates obtained a significantly greater percentage of the food in their cage (visible to them only) than the food in the doorway (visible to both competitors; Wilcoxon test: T=45, N=9, P<0.01). Of all the food obtained by subjects in the Subordinate–Door condition, 83% came from their own cage (visible only to them). The percentage of pieces that subordinates recovered from their own cages in the Subordinate–Door condition was also significantly higher than the percentage of pieces recovered in the other conditions, all of which involved pieces of food the dominant could see (either along with the subordinate or exclusively). This percentage was thus higher than the Door–Door condition (Wilcoxon test: T=36, N=8, P<0.01) and the Dominant–Door condition (Wilcoxon test: T=45, N=9, P<0.01). The overall finding is thus that subordinates obtained more food, by several orders of magnitude, when only they could see it.

On a number of occasions in the Subordinate–Door condition, subordinate individuals behaved in especially strategic ways with regard to the piece of food that only
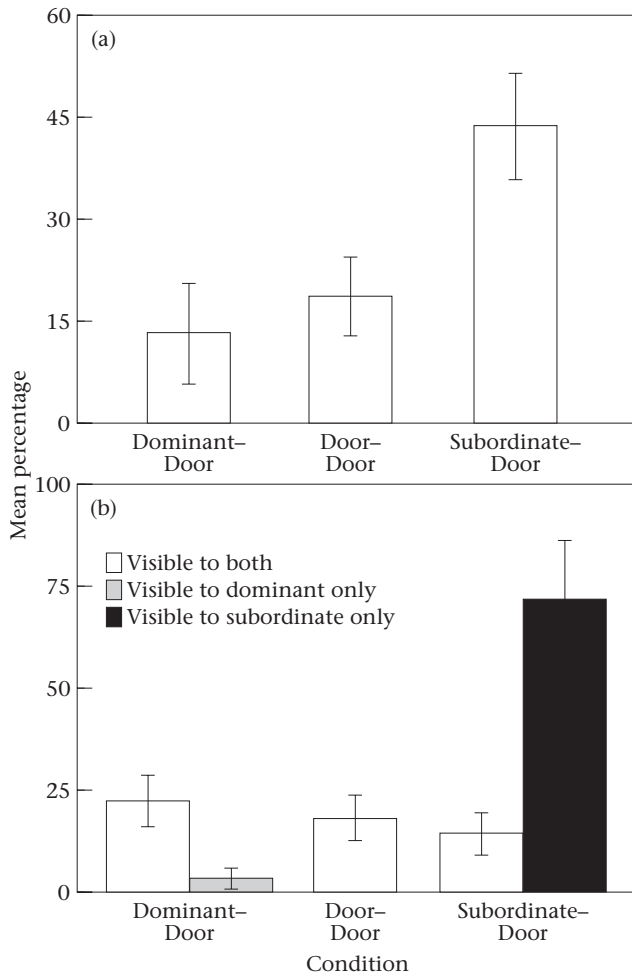
Figure 2. (a) Mean percentage±SEM of pieces of food obtained by subordinate subjects in each of the three test conditions in the wall test (experiment 1) and (b) as a function of who had visual access to the food location.

they could see. On seven occasions (five different individuals) the subordinate approached the doorway but refrained from taking the food hidden just beside it, because the dominant was in the doorway taking the food there. In each of these cases, they waited there until the dominant moved away, and then they took the food. On four occasions (involving two individuals), the subordinate was even more proactive. In these cases the subordinate came not to the doorway but to the side of the doorway, out of sight of the dominant who was just on its own side of the doorway. They then reached over and took the hidden food, all outside of the dominant's visual field.

One interesting additional piece of information concerns the dominants' behaviour in the Dominant–Door condition. In this condition, the dominant could see both pieces of food equally well and might be expected to go to either first. But they did not. In those trials in which they obtained both pieces of food (virtually all trials in this condition), dominant animals collected the piece of fruit in the doorway first in 74.8% of the trials (Wilcoxon test: $T=28$, $N=7$, $P<0.05$). This is obviously the best

strategy from a competitive point of view. By first going to the piece of food that both subjects can see, the dominant virtually ensures that it will obtain both pieces of food, whereas going to the other piece of food first puts at risk the openly visible piece in the doorway.

Discussion

Subordinate animals preferentially selected the food hidden from the dominant. This is clearly illustrated in the Subordinate–Door condition, in which the subordinate did not contest the food in the doorway that they both could see, but simply went for the food in its own cage that the dominant could not see (and was successful most of the time). Moreover, some subordinate individuals 'waited' and 'hid' in strategic ways in order to obtain the food. On the other hand, dominant individuals in the Dominant–Door condition went first to the food that both of them could see and only later for the food in their own cage, which only they could see.

Taken together, the behaviour of subordinate and dominant individuals is consistent with the idea that chimpanzees know what other individuals can and cannot see. However, two alternative explanations that do not require any sensitivity to seeing may still explain the results. The first explanation concerns accessibility to food. Although the equidistant positioning of the food between competitors in this experiment ruled out the possibility that subordinates approached the hidden food because it was closer to them, the blocked visual access also meant partially blocked physical access. That is, in the Subordinate–Door condition, the subordinate could go straight to the food in its cage, whereas the dominant had to come through the doorway and around (albeit not very far). From the outset of a trial in this condition, the subordinate might thus be able to assess that the dominant will take some time to get to the food in its (the subordinate's) cage and judge that this piece of food is therefore obtainable. Similar reasoning would direct the dominant to go first to the contested piece of food in the doorway and only later to the food in its cage that the subordinate would have difficulties in accessing physically. The strategic reasoning here is complex, but concerns only such things as travel times and blocked access, not knowledge of the visual experience of the other individual. The second alternative explanation is that subordinate individuals took the hidden food because in approaching that piece they could not see their competitor ('out of sight out of mind'). Although it is true that subordinates saw dominant animals approaching the food in the doorway, which represents an improvement over the previous experiment, the absence of the dominant at the time of picking up the food may still explain our current results.

EXPERIMENT 2: THE TYRE TEST

Although the conditions of experiment 1 represented an improvement over those in the pilot experiment, its

setting made it difficult to disregard competing explanations completely. In this second experiment, we attempted to rule out these explanations by introducing two key modifications. First, we removed the physical barrier element by blocking visual access in another way, specifically, by hiding one piece of food inside or behind a tyre equally physically accessible to both contestants, although only the subordinate animal knew the food was hidden. Second, we placed the food in a single cage to which both subjects were given equal access. In this way, the dominant was present when subordinate animals attempted to obtain the hidden food. Our prediction was that subordinate animals would preferentially select pieces of food hidden from the dominant.

Methods

Subjects

These were the same as in experiment 1 (see Table 1).

Procedure

We tested subjects by using the same general food competition paradigm as before. Pairs of dominant and subordinate animals were housed in three adjacent cages (see Fig. 3). A car tyre (70 cm diameter, 15 cm high) was situated in the centre of the middle cage (cage 2, see Fig. 3) immediately in front of the doors connected to the two extreme cages. At the beginning of each trial, each subject was confined in one of the extreme cages (cages 1 and 3, Fig. 3) while E1 introduced two pieces of fruit inside the middle cage. Food pieces were placed either on top of, inside, or next to the tyre. E1 entered the middle cage and deposited two pieces of food in one of three predetermined configurations corresponding to the three test conditions. The three test conditions varied as a function of the food location, which determined whether the dominant was able to see the food from its location once the doors were raised. The key design feature of this experiment was that subordinate individuals witnessed the baiting process, whereas dominant individuals did not. That is to say the subordinate's door in each trial was raised ca. 15 cm during the baiting process while the dominant's door remained completely closed.

(1) Inside–Top. One piece of fruit was located on top of the tyre and thus was openly visible to both subjects throughout. The second piece of food was placed ca. 50 cm to the side of the first piece tucked inside the tyre and hidden from both subjects' sight (although the subordinate had watched the hiding process and so presumably knew it was there). The food and tyre were arranged so that both pieces of food were equidistant from the subjects' starting places.

(2) Behind–Outside. One piece of food was located on the floor next to and behind (from the dominant's point of view) the tyre, and thus was visible only to the subordinate animal. The second piece was located on the floor ca. 50 cm from the first piece, away from the tyre, and so was equally visible to both subjects. The food and tyre were arranged so that both pieces of food were equidistant from the subjects' starting places.
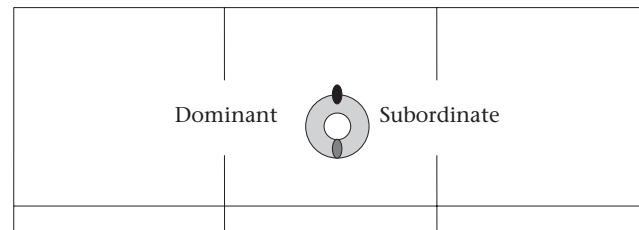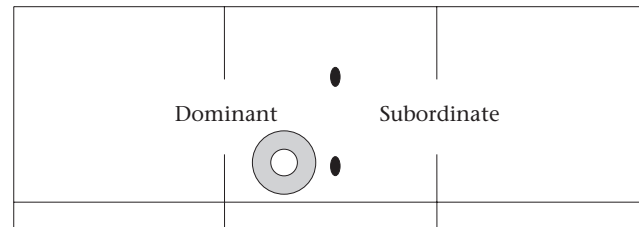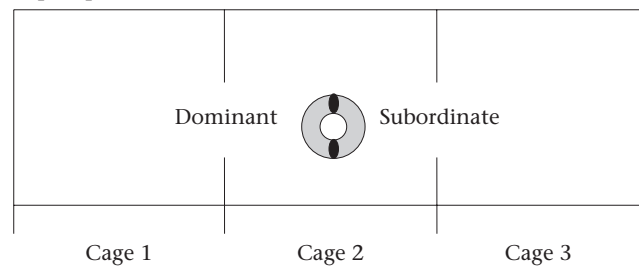

Figure 3. Experimental conditions in the tyre test (experiment 2). Both pieces of food were equidistant from the subjects.

(3) Top–Top. Both pieces of food were visible to both subjects throughout the competition as they were placed on the top on opposite sides of the tyre, separated by ca. 50 cm. The tyre was centred in the middle cage so that both pieces of food were equidistant from the subjects' starting places.

After completing the baiting, E1 left the cage and another experimenter raised the dominant's door 15 cm, so that now both animals could see the physical situation and each other (but they could not enter the middle cage). After about 5 s, when both subjects had looked through their respective doors, both doors were simultaneously raised releasing the subjects into the middle cage.

All possible pairs of subordinate–dominant animals in both groups were tested once in each condition (27 pairs × 3 conditions=81 total trials). Each pair of subjects was run in each of the three conditions one after the other, typically with one condition per day and no more than a few days between conditions. Across subjects, order of conditions was counterbalanced. Scoring and analysis were identical to those used in the previous studies (i.e. percentages were used in order to obtain one score per individual per condition).
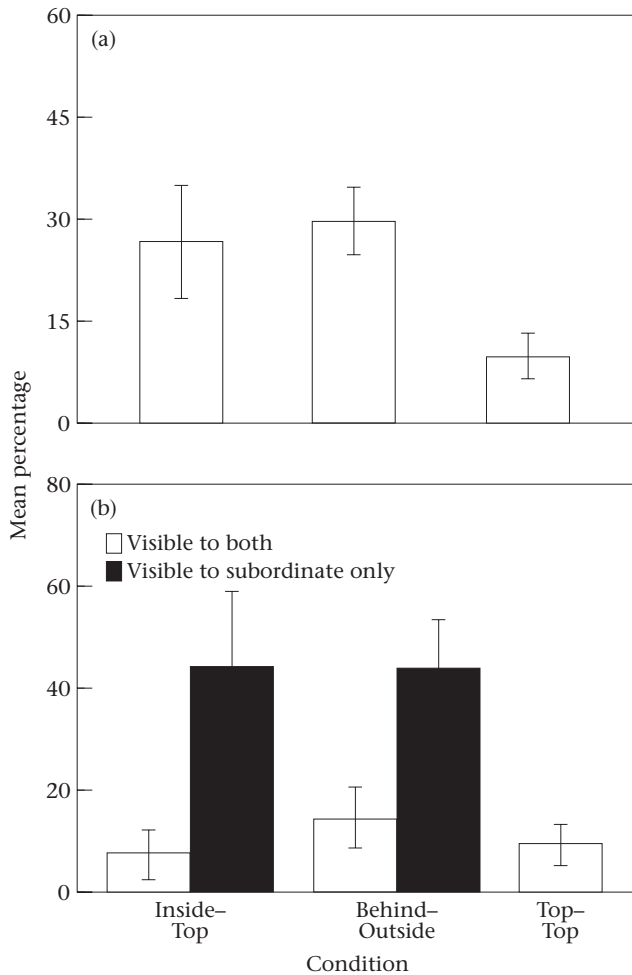
Figure 4. (a) Mean percentage±SEM of pieces of food obtained by subordinate subjects in each of the three test conditions of the tyre test (experiment 2) and (b) as a function of who had visual access to the food location.

Results

Figure 4a shows the percentage of pieces of fruit obtained by subordinates in each of the three test conditions. Overall, the difference between conditions approached significance (Friedman test: $\chi^2_2=4.5$, $N=9$, $P=0.055$). Pairwise comparisons between conditions confirmed this trend. Subordinates obtained a significantly larger percentage of pieces in both the Inside–Top (Wilcoxon test: $T=21$, $N=6$, $P<0.05$) and Behind–Outside ($T=24$, $N=7$, $P<0.05$) conditions than in the Top–Top condition. There was no difference between the percentage of success in the Inside–Top and Behind–Outside conditions.

Also important was which piece of food the subordinate obtained when it did obtain food. Figure 4b shows the percentage of pieces obtained by subordinates in each condition as a function of whether the food was visible or hidden to them and their competitor. Subordinates obtained a significantly greater percentage of the pieces that were not visible to dominants than pieces that were visible to dominants. This was true in both the

Inside–Top (Wilcoxon test: $T=25.5$, $N=7$, $P<0.05$) and Behind–Outside ($T=15$, $N=5$, $P<0.05$) conditions. Of all the food obtained by subjects in the Inside–Top condition, 85.8% came from the inside location (not visible to the dominant). Similarly, of all the food obtained by subjects in the Behind–Outside condition, 75.1% came from the behind location (not visible to the dominant). These values are both significantly higher than those in the Top–Top condition as well (for the comparison with the Inside–Top condition: Wilcoxon test: $T=27$, $N=7$, $P<0.05$; for the comparison with the Behind–Outside condition: $T=20$, $N=6$, $P<0.05$). Across all conditions, foods that were openly visually accessible to both individuals throughout all had equally low values in terms of the subordinate's success. Again the overall finding is thus that subordinates obtained more food, again by several orders of magnitude, when only they could see it.

On a number of occasions in the Inside–Top and Behind–Outside conditions, subordinate individuals behaved in especially strategic ways with regard to the piece of food that only they could see. On seven occasions (four different individuals) the subordinate individual approached the tyre but refrained from taking the food hidden inside or just behind it (from the dominant's point of view), because the dominant was close by. In each of these cases, they waited there until the dominant moved away, and then took the food. On three occasions (involving three individuals), the subordinate was even more proactive. In one case the subordinate waited until the dominant turned its back (even though it was still close by); and in two other cases the subordinate gave some active communicative signal (in one case a greeting and in the other case a sexual 'presents'), seemingly to keep the dominant on its own side of the tyre. They then reached over and took the hidden food, as their bodies blocked the dominant's line of sight to their actions.

Discussion

Subordinates obtained food reliably only when they had exclusive visual access to its location. As in the previous experiment, some subordinates also behaved in strategic ways to avoid detection when reaching for hidden food, which in two cases involved the use of more proactive social strategies. Moreover, this experiment effectively ruled out two of the alternative explanations of the previous ones. First, dominants' lack of visual access did not mean that they also had limited physical access; their physical access was equal to that of subordinates for all pieces of food in all conditions (all of which were equidistant to both individuals). Second, subordinate animals made their choices in most cases when the dominant animals were present in the same cage (ruling out the 'out of sight out of mind' hypothesis in which one individual can ignore another only if they cannot see it at the time of choosing).

Therefore, these results support the notion that subordinate individuals knew what the dominant individuals could and could not see. However, this experiment does not rule out the possibility that the behaviour of the

subordinate might have been influenced by the behaviour of the dominant. That is to say, as the subordinate approached the tyre, it may simply have monitored the dominant's intention movements. As the dominant headed for the visible food, the subordinate simply adjusted accordingly and went for the other food, to which the dominant did not have visual access. In this case, the behaviour would again have been a cognitively complex social strategy, but it would not have involved knowledge of what the competitor could and could not see. This interpretation has also been given to one of the most famous cases of so-called deception. The observation was that of Kummer (reported by Whiten & Byrne 1988) and involved a female baboon moving very slowly towards a male behind a rock, that is, behind from the point of view of a nearby male. Although this observation has been widely interpreted as a case of deception (the female knew that the dominant male could not see the target male behind the rock and so deceived him), Bernstein (1988) pointed out that the female may have simply moved incrementally towards the hidden male and monitored the reaction of the dominant male at each step of the way. In the absence of an overt physical response from the dominant, she simply continued on her way to the target male slowly and carefully, with no assessment of the dominant's visual or knowledge states. Indeed, one could even interpret the 'waiting' strategy of some individuals on some occasions in this way.

EXPERIMENT 3: THE OCCLUDER TEST

To rule out the interpretation that subordinate subjects in experiment 2 (and perhaps experiment 1) were simply reacting to the dominants' intention movements, in this experiment subordinates were given a very small temporal headstart. The question is whether they would go immediately for the food to which they had exclusive visual access, or whether, alternatively, they would go for the food openly visible to both contestants. Our prediction was that they would go for the food to which they had exclusive visual access.

Methods

Subjects

The subjects were the same as in experiments 1 and 2.

Procedure

We used the same general food competition paradigm as before. Pairs of dominant and subordinate animals were housed in three adjacent cages (see Fig. 5). One or two pieces of PVC pipe (20×25.4 cm) were used as occluders to hide food under some conditions from the dominant subjects. These occluders were placed at the extreme sides of the cages equidistant from the two competitors (food pieces ca. 2 m apart and 1.5 m from each participant). At the beginning of each trial, each participant was confined in one of the extreme cages while E1 introduced two pieces of fruit inside the middle cage. Both participants' doors were completely closed so
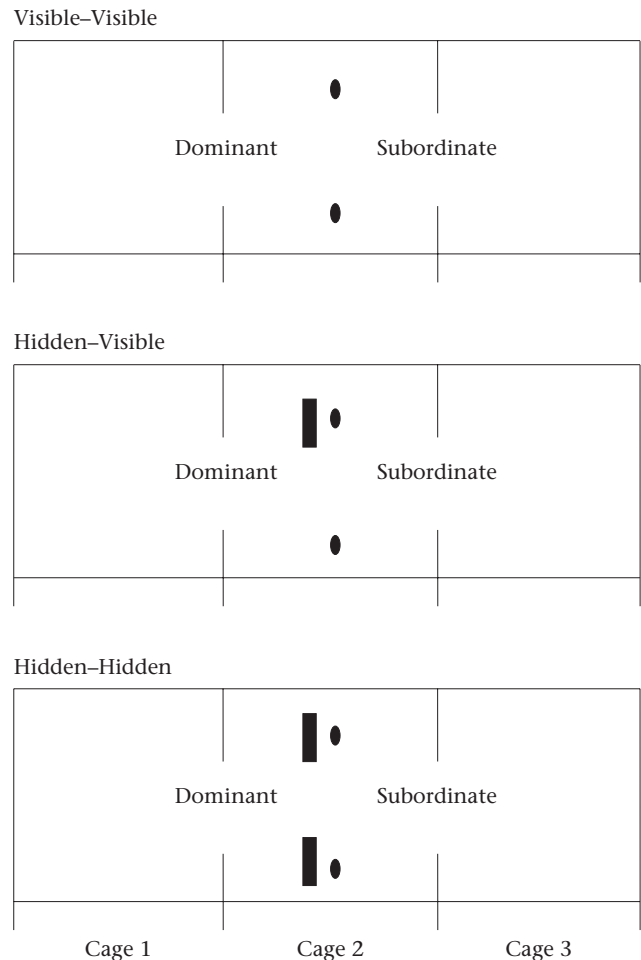

Figure 5. Experimental conditions in the occluder test (experiment 3). Both pieces of food were equidistant from the subjects.

that neither could observe the hiding process. Food pieces were placed on the floor in one of three predetermined configurations. In all of these configurations, subordinate animals could see both pieces of food, whereas dominant animals could see only some food items in only some conditions.

(1) Visible–Visible. There were no occluders inside the cage so both pieces of food were visible to both competitors throughout.

(2) Hidden–Visible. One occluder was present in the cage such that it prevented the dominant animal (but not the subordinate) from seeing one of the pieces of food.

(3) Hidden–Hidden. Two occluders were present in the cage such that they prevented the dominant animal (but not the subordinate) from seeing either of the pieces of food.

After completing the baiting, E1 left the cage and E2 raised both subjects' doors 15 cm, which allowed them to see the physical arrangement of the occluders and food and also the other participant looking under its door. Once both subjects had looked through their respective doors, the subordinate subject was released first while the dominant subject was delayed until the subordinate

began to approach one of the two food locations (ca. 1–2 s), at which point the dominant was released as well.

All possible pairs of subordinate–dominant animals in both groups were tested in each condition: once in the Visible–Visible and Hidden–Hidden conditions, and four times in the Hidden–Visible condition (twice on each side of the cage). Four trials were given in the key Hidden–Visible condition to make sure that subordinate subjects knew that the dominant would be released soon after it (the subordinate) had made its choice about which food to go for. There were thus a total of 27 pairs and 162 trials: 27, 27 and 108 trials in the three conditions. Each pair of subjects was run in each of the three conditions one after the other, typically with one session per day and no more than a few days between sessions. Across subjects, order of conditions was counterbalanced. Scoring and analysis were identical to those used before.

Results

Main results

Figure 6a shows the percentage of pieces obtained by subordinate subjects in each of the three test conditions. There were significant differences between conditions (Friedman test: $\chi_2^2=5.72$, $N=9$, $P<0.05$) such that subordinate subjects obtained more pieces in those conditions in which there were more hidden pieces (i.e. most in Hidden–Hidden, next most in Hidden–Visible and least in Visible–Visible).

Of central importance was which pieces of food (visible or hidden) subordinates obtained in the different conditions, especially the Hidden–Visible condition in which a clear choice was available. Figure 6b shows the percentage of pieces obtained by subjects in each condition as a function of the visibility of those pieces. There were significant differences between conditions (Friedman test: $\chi_3^2=12.83$, $N=9$, $P<0.01$). Pairwise tests revealed that subordinates obtained more food in the Hidden–Hidden than in the Visible–Visible condition (Wilcoxon test: $T=21$, $N=6$, $P<0.05$). Of crucial importance, in the Hidden–Visible condition subordinates obtained more hidden than visible pieces (Wilcoxon test: $T=36$, $N=8$, $P<0.01$). Of all the food obtained by subjects in the Hidden–Visible condition, 62.8% came from the hidden location.

One additional piece of information was available for this study. In anticipation of the possibility that subordinates would approach one of the foods with its headstart, and then be frightened off as the dominant was released, we also noted down for each trial which food the subordinate started out for (i.e. reached half-way to one or the other food), regardless of whether it actually obtained food. The percentage of trials in which subordinates approached ± SEM was 74.6 ± 11.1%, 76.5 ± 10.1% and 88.9 ± 11.1% in the Visible–Visible, Hidden–Visible and Hidden–Hidden conditions, respectively (Friedman test: $\chi_2^2=3.50$, $N=9$, NS). Subordinates had an especially strong preference for the hidden food in the Hidden–Visible condition. As a proportion of all trials in which an approach was shown, subordinates started out for the
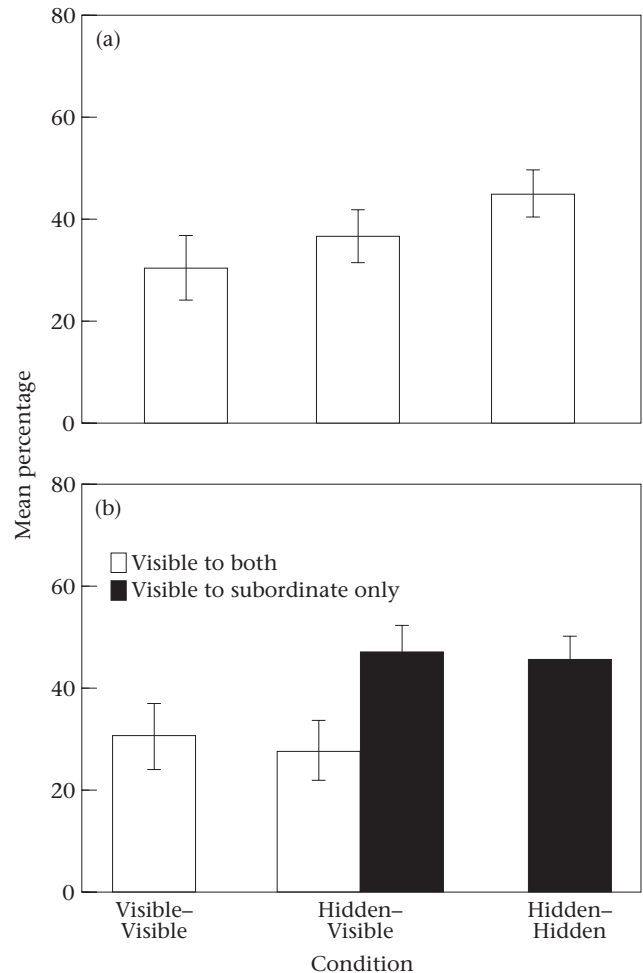

Figure 6. (a) Mean percentage±SEM of pieces of food obtained by subordinate subjects in each of the three test conditions of the occluder test (experiment 3) and (b) as a function of who had visual access to the food location.

hidden food on 73.4% of all trials (as opposed to 26.6% for the visible piece of food), a significant difference (Wilcoxon test: $T=36$, $N=8$, $P<0.01$). This is despite the fact that proportionally they were more likely to get the food when they approached the visible than the hidden food (87.1 ± 7.1% compared to 59.6 ± 8.0%; Wilcoxon test: $T=20$, $N=6$, $P<0.063$, two tailed). This finding argues against some kind of learning process in which the subordinate learned over trials to go to the hidden food because it was more easily obtainable.

On a number of occasions in the Hidden–Visible and Hidden–Hidden conditions, subordinate individuals behaved in especially strategic ways with regard to the pieces of food that only they could see. On four occasions (three different individuals) the subordinate waited until the dominant moved away, and then took the hidden food. On one occasion, a subordinate used her headstart to race over to the dominant's doorway and greet her as the door opened, effectively keeping her in her cage. The subordinate then managed to get both pieces of hidden food.

The dominant test

Because giving the subordinates a headstart creates some additional competitive problems for the dominant animal, namely, by the time the dominant gets its chance the subordinate has already moved close to its choice, we ran an additional experiment that was an exact duplicate of experiment 3 but with roles reversed. That is, the dominant animal was the one who could see both foods in the Hidden–Hidden condition and one food in the Hidden–Visible condition, and the dominant individuals got a small headstart.

Dominant individuals obtained both pieces of food on almost all trials. Analysis of the order in which they collected food in the crucial Hidden–Visible condition revealed a marginally significant difference in favour of collecting the at-risk visible piece first (Wilcoxon test: $T=6$, $N=3$, $P=0.055$), a result consistent with the findings of the dominants' behaviour in experiment 1. The weakness of this result was that over trials dominant animals seemed to learn very quickly that with a headstart they could get both pieces of food in all conditions with impunity, and thus without strategic planning. Thus, an analysis of the first trial in the Hidden–Visible condition, at which point dominants could not yet know how big an advantage they had, showed that 75% of the subjects (6/8, one subject was excluded because it did not get both food pieces) collected the visible piece first in the first trial. Preference for one or the other piece of food as the first one chosen then went down over trials.

Comparing the collection order in the Hidden–Visible condition in experiment 3 and this one revealed that dominant subjects collected visible pieces first in $67.7 \pm 15.5\%$ of the trials whereas the same individuals playing the role of subordinate collected visible pieces first in $38.4 \pm 9.1\%$ of the trials. Although this seemed to suggest that subjects reversed their choice pattern depending on the role played (dominant or subordinate), there were no significant differences between the percentage of trials in which subjects targeted the visible piece first when playing as dominants as opposed to subordinates (Wilcoxon test: $T=12$, $N=5$, NS).

Discussion

As in the previous experiments, subordinates chose to go most often to the hidden food, that is, the food that the dominant could not see. The design in which the subordinate was able to move towards one choice before the dominant animal was released ruled out the possibility that subordinate animals were merely reacting to the dominant's intention movements in gauging their choices. It is also noteworthy that when the same subjects were used in the dominant role, they tended to change their strategy by targeting the visible pieces first, which is reminiscent of the strategy used by dominants in experiment 1 when they took the most at-risk visible food first, and only later went for the less contestable hidden food. These results are thus best explained by the hypothesis that chimpanzees know what others can and cannot see, at least in this experimental situation, and they use that knowledge to guide their own foraging choices.

However, there is still one alternative hypothesis. Subordinate individuals could see the dominant looking out from under their door as they made their choice. It is thus possible that they established the dominant's visual gaze direction and then, based on past experience in which they tried unsuccessfully to get food that a dominant was looking at, chose the food the dominant was not looking at, what might be called the intimidation hypothesis. Given our experimental arrangement, we were unable to monitor the dominant's behaviour during the subordinate's choice, but it should be noted that the crack in the door did not offer a full view of where the dominant was looking, and indeed in some cases it was clear that the dominant was not looking under the door while the subordinate was making its initial move. Nevertheless, this hypothesis is a viable alternative that must be assessed, which we did in two different ways in the next two experiments. In a control we assessed the possibility that subordinates simply prefer going to the location with the occluder for some irrelevant reason.

EXPERIMENT 4: CONTROLS FOR OCCLUDER TEST

Dominant Door Down

We first simply replicated the occluder test, except that in this case we kept the dominant's door closed during the subordinate's choice period so that there could be no 'intimidation' or other cues coming from the dominant.

The method was the same as in the main occluder test of experiment 3 in all respects with two exceptions. First, a 9-month period elapsed between the other experiment and this one (and this also applies to the controls that follow this one). We therefore felt it necessary to reassess dominance relations, as these can change in this length of time. There were two changes detected, and so the new pairings reflected these changes. Second, the way doors were opened and closed was changed to fit the needs of this control test. Specifically, after E1 had set up the occluders and food as required for a given condition, E2 first raised the dominant's door for some seconds. He then closed that door and opened the subordinate's door slightly. The subordinate was then released, with the dominant released after the subordinate had made its initial move in one direction or the other, as in the experiment 3 occluder test. Overall, there were 27 pairs and 162 trials run, with counterbalancing, scoring and analysis as before.

Results replicated those of the experiment 3 occluder test, thus falsifying the intimidation hypothesis. Specifically, as in experiment 3 there were significant differences between conditions such that subordinate subjects obtained more pieces in those conditions in which there were more hidden pieces (Friedman test: $\chi^2_2=8.67$, $N=9$, $P<0.007$). Pairwise comparisons revealed that subordinates obtained more food in the Hidden–Hidden condition (52.8% of the time) than in the Visible-Visible condition (31.3% of the time; Wilcoxon test: $T=21$, $N=6$, $P<0.014$). This pattern held for six of the nine individuals, with no individual showing the opposite pattern (three ties).

Of central importance was which pieces of food (visible or hidden) subordinates chose in the Hidden–Visible condition (an overall success rate of 41.9%). In the Hidden–Visible condition subordinates obtained more hidden than visible pieces (Wilcoxon test: $T=27$, $N=7$, $P<0.017$). Of all the food obtained by subjects in the Hidden–Visible condition, 58% came from the hidden location and 42% from the visible location. In all, six individuals preferred the hidden food, one preferred the visible food, and two showed no preference. This finding also held for approaches in the Hidden–Visible condition. Again, subordinates approached the hidden piece of food more often than the visible piece (Wilcoxon test: $T=21$, $N=6$, $P<0.014$).

Dominant Visual Cues

As a second control test for the intimidation hypothesis, we also ran an experiment in which both competitors looked simultaneously out at the food configuration, but in this case it was the dominant who could see where the food was located (and the subordinate again got a head-start). We therefore took the 'opposite' approach to the previous test in that we assessed directly whether the subordinate could use cues from the dominant's behaviour to locate the food, either to take it or to avoid it.

Subjects and pairings were the same as before (with the exception that one individual could no longer be tested; total=21 pairs and 132 trials). We changed the experimental arrangement so that the food, always one piece, was placed on the dominant's side of the two occluders so that only the dominant individual had visual access to the food. There were two experimental conditions. In one, both subjects had their doors raised so that both could see the occluders, but only the dominant could see the piece of food behind one of the occluders; the subordinate could thus potentially read the dominant's behaviour and locate the food. In the other, only the subordinate's door was raised, so that there was no opportunity to read the dominant's behaviour. If the subordinate used the dominant's behaviour to locate the food, either to go for it or to avoid it, then the two conditions should differ from one another in some way.

The subordinates did not use the dominants' behaviour to locate food in this study, choosing the baited location 50.9% of the time and the unbaited location 49.1% of the time when the dominant's door was raised, statistically identical to chance by a Wilcoxon test (and indeed they had slightly better success, although still at chance, in the other condition with no competitor cues at all). No individuals showed reliable strategies that differed between the two conditions. And this was not because their choices did not matter; when they guessed the food location correctly they obtained the food almost three times as often as when they guessed incorrectly (75 to 26%).

Subordinate Preferences

There is one further alternative hypothesis for the experiment 3 occluder test. In the occluder test (and also in the Dominant Door Down control), subordinates may simply have preferred the piece of food with the occluder, perhaps because it appeared closer or more accessible. There is no evidence for this hypothesis, and indeed we consider it highly unlikely because when they were in the dominant role, subjects preferred to take the visible pieces (associated with no occluder). Nevertheless, we tested this hypothesis explicitly.

Subjects were assessed for their preferences in a non-competitive situation. There was one piece of food out in the open (as in the Visible condition of the occluder test) and one piece of food on their side of an occluder (as in the Hidden condition in the occluder test). The rest of the procedure was as in the other studies (door raised briefly and then subject released), with nine individuals completing eight trials each. The main result was that subjects showed no preference for either piece of food, with 50% of the pieces in front of the occluder (Hidden) chosen and 50% of the pieces out in the open (Visible) chosen.

Discussion

The first two control studies provide no support for the hypothesis that subordinates in the main occluder test in experiment 3 used the dominant's behaviour as a cue for which piece of food to avoid. In the Dominant Door Down control, subordinates behaved just as they did in the main occluder test, even though they could not see the dominant's behaviour at all. In the Dominant Visual Cues control, subordinates did not use the dominant's behaviour as seen under the door to locate the food, even though it would have been to their advantage to do so. The most plausible hypothesis is thus that in the occluder test, as well as in the Dominant Door Down control, subordinates based their foraging choice on what the dominant could and could not see (which indicated where it would go). The third control established that the subordinate's behaviour was not due to some a priori preference for going to the location with a barrier.

EXPERIMENT 5: THE TRANSPARENT BARRIER

In a final experiment we tried a different kind of occluder, to see what subordinates would do in the occluder test if the occluder was a transparent barrier that did not occlude the dominant's vision at all. This experiment addressed two main issues. First and most obviously it further tested the subject's understanding of visual perception, barriers to visual perception, and how they interact. If subordinates truly understand something of the mechanics of visual perception they should understand that the transparent barrier does not occlude the dominant's vision, and so they should choose randomly between the two food locations. If they behaved in this way, it would demonstrate their ability to adjust their behaviour flexibly in this experimental situation dependent on the competitor's visual access as determined by different types of barriers; and these are just the kinds of flexible adjustments that normally indicate complex cognitive processes as opposed to blind and inflexible

behavioural rules (Tomasello & Call 1997). Second, this experiment also served to rule out another unlikely but still possible alternative hypothesis for the occluder test. In that test subordinates might have thought not that the occluder blocked the dominant's vision, but only that it made it harder to reach the food (because the dominant had to reach around the occluder). In experiment 5 the occluder was transparent and so it served as an obstacle to the dominant's reaching in exactly the same way as the occluders in the previous studies, while not actually blocking its vision. If subordinates indeed believe that barriers make it harder for dominants to reach the food, then they should prefer to go for the food located there (as in the other occluder tests); if not, as we predicted, then they will presumably choose randomly.

Subjects were the same as in the three controls, with the exception that two new subjects (Georgia and Natasha) had become available and so were included in testing (their behaviour was not distinctive in any way). The test situation was the same as before with the exception that we ran two rounds of trials with different delays between the release of the two competitors. In the first round we delayed the dominant's release until after the subordinate had chosen one or other piece of food (as in the Subordinate Preferences control experiment). In a second round we released the dominant just after the subordinate had chosen a direction (as in the occluder experiments).

With the longer delay between releases, subordinates showed no preference for the food behind the transparent barrier (55%) or the piece in the open (45%) (Wilcoxon test: $T=14$, $N=5$, NS). With the shorter delay, subordinate subjects showed a small preference for the piece of food in the open (57 to 43%; Wilcoxon test: $T=49$, $N=10$, $P<0.028$, two-tailed). We have no ready explanation for the subjects' preference for the food in the open in this second round of testing, but the main point is that they did not prefer the transparent barrier and so they clearly did not think that the plastic bottle was occluding, or in any other way hindering, the vision or behaviour of the dominant.

GENERAL DISCUSSION

Our experiments establish that at least in some situations chimpanzees know what conspecifics do and do not see and, furthermore, that they use this knowledge to formulate their behavioural strategies in food competition situations. This finding helps to resolve a puzzle in the recent literature. Chimpanzees show strong and robust skills in following the gaze direction of others, including to locations behind barriers, behind themselves and past distractors (Povinelli & Eddy 1996a; Tomasello et al. 1999); they even check back with the looker when their gaze following leads to no interesting sights (Call et al. 1998). However, in simulated foraging situations in which a human or conspecific attempts to help them find hidden food through gaze cues or other forms of communication, chimpanzees have shown weak and somewhat fragile skills (Povinelli & Eddy 1996c; Call et al. 1998; Itakura et al., in press). If our findings are reliable,

they suggest that perhaps the communicative situations of these latter studies may be unnatural for chimpanzees, who have not evolved for this kind of cooperative communication over monopolizable food resources and who do not normally experience in their individual ontogenies others helping them to find food, and thus that chimpanzees' most sophisticated social-cognitive abilities may emerge only in the more natural situation of food competition with conspecifics. Indeed it is notable that our chimpanzees did not have to be trained in any procedures nor did they have to interact with humans at any time during the testing, which would seem to provide a priori evidence that our paradigm is a very natural one in which to assess primate social-cognitive skills.

Operationally, the finding was that in food competition situations subordinates chose to go for food that dominants could not see rather than food that they could see. This strategy did not depend on the dominant individual being visually absent ('out of sight out of mind') when the subordinate made its choice (the tyre test of experiment 2), or on the subordinate's monitoring of the behaviour of the dominant during the choice (the occluder test of experiment 3), or on their monitoring the dominant's visual behaviour from behind the partially closed door (the Dominant Door Down and Dominant Visual Cues tests of experiment 4). Moreover, when presented with a transparent barrier placed so that it would, if it were solid, block the view of the dominant, subordinates knew that in reality it did not (experiment 5). Chimpanzees' strategically appropriate behaviour with the transparent barrier was perhaps especially important since they had not had much experience with transparent objects previously and so could not have had many opportunities to learn specific contingencies between these objects and the behaviour of their groupmates.

It is noteworthy that in all of the tests some subordinates in some trials engaged in strategic manoeuvring such as waiting or hiding to obtain pieces of food, sometimes even using more proactive strategies such as distracting the dominant away from the hidden food. In addition, the majority of individuals behaved very differently when they played the role of dominant (which the majority of individuals did on multiple occasions). In two different studies dominants tended to go first for those pieces of food that were openly visible to both competitors and only later for the hidden piece that only they could see (experiments 1 and 3), the opposite behaviour to that they displayed as subordinates. This strategy of the dominants makes sense because it ensured that they first got the piece of food the subordinate could see (and so was likely to go for), which allowed them later, at their leisure, to take the piece that only they could see. The fact that the same individuals adopted different strategies depending on the role they played in the experiment, subordinate or dominant, suggests that they were not following some blind behavioural contingencies or rules, but rather that they really did understand something of the situation from a social-cognitive point of view.

Our results do not help to resolve the discrepant findings concerning chimpanzees' and other nonhuman

primates' understanding of higher level mental states such as thinking, believing and intending, that is, their 'theory of mind' narrowly defined. They concern chimpanzees' understanding of visual perception only. However, even if it is true that chimpanzees know what other individuals can and cannot see, there are still multiple possibilities for the nature of this understanding, some more mentalistic than others. For example, the cognitively strongest hypothesis is that chimpanzees understand the visual perception and experience of others in much the same way as humans. That is, an individual understands that: (1) others see things that it does not currently see (e.g. because of occlusion); (2) others can have different perspectives on the same object it is now perceiving (e.g. from a different angle); and (3) the visual experience of the other is similar to its own (i.e. an individual can simulate the visual experience of others by imagining how it would see it if in the other's place). On the other hand, the cognitively weakest hypothesis is that the chimpanzees' behaviour in our experiments is based on learned behavioural contingencies, accompanied by no understanding of the other's visual experience at all.

We do not believe that either of these extreme hypotheses is true. First, we do not believe that chimpanzees understand visual perception in the same manner as humans (especially the analogy to the self) because they showed no evidence of such understanding in a variety of other studies of social cognition (see Tomasello & Call 1997 for a review). But we also do not believe that all that is involved is some form of noncognitive behavioural conditioning. As is often the case in post hoc behaviouristic explanations, to account for our findings this cognitively weak hypothesis would have to posit different sets of learned contingencies in virtually every experiment (and indeed different sets of contingencies for the subordinate and dominant roles in each experiment), including the transparent barrier test, which involved an 'occluder' with which subjects had had very little experience. Such post hoc scenarios, based on no actual observations of individuals' behaviour, seem highly unlikely.

There are still other hypotheses that are weaker than the 'full human understanding' hypothesis but nevertheless stronger than the 'blind contingencies' hypothesis, and that account for the data better than either. Our mixed hypothesis is that chimpanzees have some natural tendencies to follow the gaze of others (as do many other primate species; Tomasello et al. 1998) and they also have some natural social cognitive skills to understand and predict many aspects of the behaviour of others, for example, what they will do when food is available, what they will do when a predator is coming, what they will do when a dominant approaches, where they are going when they are locomoting in a certain direction at a certain time of day, and so forth (e.g. Menzel 1971, 1973, 1974). During their ontogenies, as they follow the gaze and attempt to predict the behaviour of others in many situations, individuals may learn many additional things about the relation of their groupmates' visual access to objects in the environment and its implications for their (their groupmates') subsequent behaviour. Thus, individuals may learn about occluders and the visual access of

others via situations in which they: (1) notice and follow the gaze direction of another individual (and also notice its behaviour); (2) see a barrier of some sort; and (3) subsequently see the target of the other's gaze because the barrier moves, the target moves, or they themselves move around the barrier (Tomasello et al. 1999). This situation should be fairly frequent in the lives of group-living animals, with groupmates themselves often being the occluding object. During these learning experiences the observer may sometimes see that the other individual is afraid or is excited about something (and so avoiding or approaching it) which the observer cannot initially see (e.g. because someone or something is occluding its view) but which it then comes to see later. Such situations provide experience for making the connection between visual access and the behaviour of others in various social contexts.

The basic idea is thus that chimpanzees naturally follow gaze and attempt to predict behaviour, and then through individual experience come to know important additional things about the relationship between the visual access of others, its likely target, and how this relates to their behaviour in a variety of different situations. It is important to emphasize that our mixed explanation is not equivalent to a behavioural conditioning, noncognitive explanation. Even though it involves learning, it may be construed as a cognitive form of learning which leads to real understanding and insight, as expressed in knowledge that is flexibly displayed in behaviour.

Thus, we do not believe that the only explanatory alternatives are blind conditioning and theory of mind, as they are often presented (e.g. Byrne 1995, 1997; Heyes 1998). Following Tomasello & Call (1997; see also Call, in press), we prefer a third alternative, namely, that individuals may have insight into social problems in the same way that they have insight into physical problems such as tool use or spatial reasoning, with this insight in all cases depending to some degree on personal experience with the objects and activities involved. On a daily basis chimpanzees find themselves in novel social situations for which they devise novel strategies, or adapt known strategies, based on a knowledge of the structure of the social problem. In our experiments this knowledge included the knowledge of what conspecifics could and could not see, that is, knowledge of which things in the environment their competitor did and did not have visual access to, and they used this knowledge to predict how the dominant would behave when its door was opened. This scenario does not imply that chimpanzees understand that the visual experience of others is in some sense analogous to their own, as in the human case, but it does imply a flexible understanding of how others work as animate beings; in particular, it implies an understanding that the behaviour of others is determined in some specific ways by what they do and do not have visual access to.

Our finding that chimpanzees know what conspecifics can and cannot see, and that they use this information flexibly in certain competitive situations, thus adds to our understanding of the social cognitive processes that

underlie primate social behaviour and helps to explain the extraordinary complexity of primate social life.

Acknowledgments

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