

ORIGINAL ARTICLE

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Chimpanzee gaze following in an object-choice task

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Abstract Many primate species reliably track and follow the visual gaze of conspecifics and humans, even to locations above and behind the subject. However, it is not clear whether primates follow a human's gaze to find hidden food under one of two containers in an object-choice task. In a series of experiments six adult female chimpanzees followed a human's gaze (head and eye direction) to a distal location in space above and behind them, and checked back to the human's face when they did not find anything interesting or unusual. This study also assessed whether these same subjects would also use the human's gaze in an object-choice task with three types of occluders: barriers, tubes, and bowls. Barriers and tubes permitted the experimenter to see their contents (i.e., food) whereas bowls did not. Chimpanzees used the human's gaze direction to choose the tube or barrier containing food but they did not use the human's gaze to decide between bowls. Our findings allowed us to discard both simple orientation and understanding seeing-knowing in others as the explanations for gaze following in chimpanzees. However, they did not allow us to conclusively choose between orientation combined with foraging tendencies and understanding seeing in others. One interesting possibility raised by these results is that studies in which the human cannot see the reward at the time of subject choice may potentially be underestimating chimpanzees' social knowledge.

Key words Gaze following · Theory of mind · Chimpanzees · Joint visual attention · *Pan troglodytes*

Introduction

Human infants show a special sensitivity to social stimuli which is demonstrated by their inclination to imitate the actions of people over the actions of objects (Legerstee 1991; Meltzoff 1995) and to engage in protoconversations with their caretakers (Bateson 1979). Furthermore, infants often use social companions to interpret and obtain information about their surroundings. For instance, when confronted with ambiguous stimuli, infants check the emotional reactions of their companions to interpret the nature of those stimuli (Campos and Stenberg 1981). Human infants can also use their social companions to locate novel stimuli. One important mechanism in this regard is gaze following. Upon seeing a human caretaker staring in a certain direction, children by the age of 18 months are capable of following her line of sight to discover novel stimuli even when these are situated behind them (Butterworth 1991).

Many primate species also reliably track and follow the visual gaze of conspecifics, even to locations above and behind the subject. Fieldworkers have provided a number of anecdotal observations of this skill, but most importantly Tomasello et al. (in press) reported experimental evidence for primate gaze following in tests using sooty mangabeys (*Cercocebus torquatus*), chimpanzees (*Pan troglodytes*), and three species of macaque (*Macaca mulatta*, *M. nemestrina*, and *M. arctoides*). Some primate species, primarily great apes, have also shown the ability to follow the gaze of human beings. Povinelli and Eddy (1996) reported that six juvenile chimpanzees followed a human experimenter's gaze to a location above and behind them, and Itakura (1996) confirmed this result with a different group of chimpanzees and one orangutan (*Pongo pygmaeus*). However, Itakura (1996) did not find a similar skill in nine different species of primate (two species of lemur, three species of New World monkey, and four species of macaque).

A different experimental paradigm has also been used to assess primate understanding of human gaze. The basic

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task consists of a human hiding some food under one of two containers and then attempting to cue individuals to the location of the food by staring at the baited container (sometimes other cues are used as well). Once again in this situation, monkeys (specifically, capuchin monkeys, *Cebus apella*, and rhesus macaques) did not use the human's gaze direction to select the correct container (Anderson et al. 1995, 1996). Call and Tomasello (1998, experiment 3) found that neither chimpanzees nor orangutans followed a human's gaze to the correct container in this task.

All of these results are consistent with a so-called "low-level" cognitive model of primate gaze following. In one formulation of this model, primates develop a tendency during ontogeny (mechanism unknown) to look in the direction that others are looking (for most individuals conspecifics only, but for others humans as well). They look in this direction until they see something interesting or important, at which point they stop. Individuals are not in any case understanding or making inferences about the attentional or mental states of others. There is one study, however, that suggests the possibility of some higher-level cognitive processes. In an experiment by Povinelli and Eddy (1996) a human experimenter faced a chimpanzee as it entered a test room to beg for food through the Plexiglas wall (as it had been trained to do in this situation). The experimenter then immediately stared in a particular direction although a solid partition affixed to the Plexiglas wall was in the experimenter's line of sight. If the partition had not been there, the experimenter's focus would have been on the back wall of the room, behind the subject. The reasoning was that if the chimpanzees were simply using gaze direction as a cue that something interesting was somewhere along the human's line of sight, they should follow that line of sight all the way to the rear of the room. However, if they stopped and inspected the partition, the inference was that they must know that the human's sight line to the rear of the room was blocked. The subjects did look to the partition more than they looked to the back wall. However, Tomasello and Call (1997) argued that perhaps the chimpanzees simply saw the partition as an interesting object in its own right, and so stopped when they saw it. The key factor in making a higher-level interpretation would be chimpanzees' attempts to look at the human's side of the partition, since this would demonstrate an appreciation of precisely what the human was looking at. Unfortunately, although Povinelli and Eddy (1996) report the occurrence of this behavior, there was no statistical comparison of subjects' looks at the experimenter's side of the partition as opposed to their own side of the partition.

In the current series of experiments we attempted to explore chimpanzees' understanding of human gaze by presenting them with several variations of the tasks used by Povinelli and Eddy (1996) and Anderson et al. (1995, 1996). In the first experiment we simply looked up and behind the chimpanzees to see if they would follow a human's gaze. Unlike previous studies, however, we also checked to see whether, when there were no interesting

objects in the human's line of sight, chimpanzees would look back to the human – since checking behavior has been taken by some investigators as evidence that human infants and apes understand more about adult gaze than its function as a discriminative cue (e.g., Butterworth and Cochran 1980; Gómez 1990; but see Corkum and Moore 1995, for a low-level model of infant gaze following). In the next three experiments we presented chimpanzee individuals with an object-choice task in which a human hid food in one of two containers and then stared at that container to cue the subject as to the food's location. In experiment 2 the food was hidden under an opaque bowl, a situation in which chimpanzees have had difficulties in the past (Call and Tomasello 1998). It is possible, however, that chimpanzees have difficulties in this situation because it is not really a gaze-following situation at all; the human is not really looking at any food and the chimpanzee might appreciate this fact. Therefore, in experiment 3 the food was hidden inside a tube so that the human was in fact looking at the food when he gave the cue. Subjects could also look into the tube from their end – opposite to the end into which the human stared – in an attempt to follow the gaze, although they could not themselves see the food. Experiment 4 duplicated this basic situation with the tube but in this case the food was hidden behind a solid partition so that again the human was looking at the food when he gave the cue, but in this case subjects were not in a position to look behind the partition themselves.

Experiment 1

The goal of this experiment was to assess whether chimpanzees would follow a human's gaze (head and eye direction) to a distal location in space above and behind them. Also of interest was whether subjects looked back at the human's face (i.e., checked back) if they could not detect the apparent target of his attention.

Method

Subjects

Six adult female chimpanzees (mean age = 26.2 years) housed in social groups at the Yerkes Regional Primate Research Center participated in this experiment (Table 1). Two chimpanzees (Peony and Tai) were wild-born and four (Jesse, Cissie, Sonia, and Ericka) were captive-born. In addition, Peony and Ericka received extensive human contact during their upbringing. Peony joined a project on language development and cognition at 2 years of age where she remained until early adolescence (see Premack 1976; Premack and Premack 1983 for additional details). Ericka was raised in a human home and later transferred to the Rumbaugh's laboratory (D. M. Rumbaugh, personal communication) where she participated in their language

Table 1 Age, sex, birthplace, rearing, and experimental histories (1 object permanence, 2 tool use and social learning, 3 comprehension of communicative signs, 4 distinguishing intentional from accidental actions, 5 false belief task, 6 language acquisition) of the subjects included in the experiment

Subject	Age (years)	Sex	Birthplace	Rearing history	Experimental history
Jesse	15	Female	Captivity	Nursery	1, 2, 3, 5
Cissie	21	Female	Captivity	Nursery	1, 3, 4, 5
Peony	29	Female	Wild	Nursery-home	6
Tai	30	Female	Wild	Mother	1, 3, 4
Ericka	24	Female	Captivity	Home	1, 3, 4, 5, 6
Sonia	38	Female	Captivity	Unknown	1, 4, 5

acquisition project until early adolescence. Peony and Ericka were transferred to the Yerkes Primate Center during adolescence and each of them was integrated into a pre-existing group of chimpanzees where they have remained until the present study took place. Prior to this study some chimpanzees had participated in other studies such as object permanence, tool use, comprehension of novel communicative signs, and theory of mind (Table 1). Only females were used because males were not available at the time this study was conducted. Testing was conducted in an indoor area adjacent the subjects' outdoor enclosures, with individuals separated from their cagemates during testing. Subjects were fed twice a day on a diet of fruit, vegetables, and monkey chow, according to their normal routine. Water was available ad libitum and subjects were not food-deprived at any time.

Procedure

A human experimenter (E) sat on a stool in a predetermined location by the cage fencing facing the subject. Subjects usually approached the experimenter and sat facing him as soon as he moved the stool to that particular location and sat on it (E had used this location when testing the subjects for other research projects, and consequently, subjects were used to receiving food there). In case subjects failed to sit in that particular location, the experimenter attracted them by holding a food reward (i.e., grape) in his hand. As soon as the subject sat facing E, he hid the food reward in his hand and initiated a trial. In each trial, the experimenter engaged in one of two conditions for a 10-s period. In the no-gaze condition (control trials), the experimenter simply stared at the chimpanzee with a neutral face for 10s. In the gaze condition (experimental trials), the experimenter looked up (by orienting his head and eyes) toward the ceiling to an imaginary point directly above the chimpanzee's head. A second experimenter (situated 3 m behind with his back turned away from both of them) timed the onset and the completion of the trials. The experimenter conducted two 6-trial blocks in a single session for a total of 12 trials. There was a 30-min break between the first and the second block of trials.

Each block consisted of a series of three control and three experimental trials presented alternately. Half of the subjects started their series with a control trial while the other half started their series with an experimental trial. The experimenter offered food rewards to the subjects after the completion of each trial regardless of their performance in order to keep them in the appropriate location for conducting the subsequent trials.

All trials were videotaped in such a way that E's behavior was not visible on the tape. One of the experimenters scored each trial on the videotapes without knowledge of the experimental condition for that trial. The experimenter watched the tape and recorded whether the subject looked to the ceiling (i.e., tilted her head backwards and looked up) during each trial. A second observer independently scored 20% of the trials (approximately equal numbers across subjects), and interobserver reliability with the main observer was excellent (Cohen's $\kappa = 0.87$).

Results

As seen in Table 2, subjects looked up to the ceiling more often in the gaze condition than in the no-gaze condition (Wilcoxon test: $Z = 2.21$, $P < 0.02$, one-tailed). Subjects looked up to the ceiling in 75.0% of the trials in which the experimenter himself was looking up (mean = 4.5 out of 6, $SD = 1.5$), but only in 8.3% of the trials in which the experimenter was staring at the subjects (mean = 0.5 out of 6, $SD = 0.8$). Three subjects (out of six) continued following E's gaze in the experimental trials at the same levels during the first and second blocks of trials while the remaining three subjects decreased their responses (presumably because they never saw anything on the ceiling). Overall there was a trend toward lower response over trial blocks (Wilcoxon test: $Z = 1.63$, $P = 0.051$, one-tailed).

Also of interest were subjects' responses to the fact that there was nothing on the ceiling when they looked. We scored three alternatives, from least indicative to most indicative of a high-level model of the subject's compre-

Table 2 Subjects' performance in the different conditions across the four studies. For experiment 1, the frequency of trials in which subjects gazed at the ceiling is shown. The highest score possible in each cell is 6. For experiments 2-4, the frequency of correct choices is reported. The highest score possible in each cell is 12; chance responding in each cell is 6; above-chance responding in each cell is 10 correct, one-tailed

Subject	Experiment 1		Experiment 2	Experiment 3		Experiment 4	
	Control	Experiment	Bowl	Bowl	Tube	Bowl	Barrier
Jesse	0	2	6	6	6	3	9
Cissie	0	4	6	7	9	11*	8
Peony	0	4	9	10*	11*	8	9
Tai	0	6	5	4	11*	6	7
Ericka	1	6	9	9	11*	7	9
Sonia	2	5	6	8	10*	5	7

Table 3 Location where subjects looked after staring at the ceiling following the experimenter's gaze in the experimental trials. Subjects' most complex behavior is shown for each trial, and the number of occasions (in parentheses) in which these behaviors appeared in the first trial of each of the two testing sessions

Subject	Location after looking at the ceiling		
	Not face	Face	Face and ceiling
Jesse	1 (0)		1 (1)
Cissie	2 (0)	2 (2)	
Peony	2 (0)		2 (2)
Tai	1 (0)	4 (2)	1 (0)
Ericka	5 (1)	1 (1)	
Sonia	4 (2)		1 (0)

hension of the mental significance of E's gaze: (1) looking anywhere except E's face; (2) looking back at E's face; and (3) looking back at E's face and then back again to the ceiling. Table 3 presents subjects' most complex behavior for each trial in which they looked to the ceiling in the experimental condition. All subjects looked back at the experimenter's face after not detecting anything noticeable in at least one trial. In addition, five of the six subjects checked E's face in the first trial in one (Ericka, Jesse) or both (Tai, Peony, and Cissie) of their two blocks of trials.

Discussion

In experiment 1 we found that chimpanzees followed a human's gaze to a location on the ceiling of their cages, replicating the findings of previous studies with chimpanzees (Itakura 1996; Povinelli and Eddy 1996). The levels of gaze following in the current experiment were higher than those reported by Povinelli and Eddy (1996). In the current experiment chimpanzees followed the experimenter's gaze in 75% of the trials, as compared with approximately 50% of the trials in that experiment. The age of the chimpanzees (5- to 6-year-olds in Povinelli and Eddy 1996, to adult chimpanzees in the current experiment), and the order and setting in which the trials were administered constitute methodological differences that may have contributed to this discrepancy. On the other hand, the level of gaze following in the current experiment was quite comparable to that reported for a different group of chimpanzees as they followed their conspecifics' gaze (Tomasello et al. 1998).

The detailed analysis of the locations where individuals looked after staring at the ceiling revealed that all subjects checked back at the experimenter's face on at least one occasion. Although checking and gaze alternation have been described in chimpanzees for communicative gestures (Tomasello et al. 1994), social referencing (Russell et al. 1997), and joint attention episodes (Carpenter et al. 1995), they have never been described in the context of gaze following. Especially informative were the cases in which subjects checked E's face and looked up for a second time to the location where the experimenter was look-

ing. One interpretation is that this checking behavior is similar to the checking behavior of human infants, which most investigators take to be an indication that infants understand something of the mental significance of adult gaze (Scaife and Bruner 1975; Butterworth and Cochran 1980). However, Corkum and Moore (1995) disagree with this mentalistic interpretation for human infants and point out that simpler processes may explain this checking behavior, for example, processes involving children's expectations of adult behavior in particular situations. In the current experimental situation, looking to the experimenter was the normal behavior in this interaction (e.g., that is how every trial began, and when the experimenter has food subjects often check to see if it is available for them), and so it is possible that what we have called checking is simply subjects returning to their normal visual orientation after having followed E's gaze to the ceiling (and second looks to the ceiling simply represent the subject's following of E's gaze a second independent time). It is impossible to choose between these two interpretations on the basis of these data alone.

Experiment 2

The previous experiment had shown that chimpanzees were capable of following the experimenter's gaze to a location above themselves. In this experiment we further investigated the chimpanzees' ability to apply their gaze-following skills to obtain food. In particular, we investigated whether chimpanzees were capable of using a human's head (and eye) orientation to identify the one opaque container (out of two) that contained food. After hiding the food under one container, the experimenter stared at the correct container and the subject was permitted to make a single selection.

Method

Subjects

The subjects were the same as in experiment 1.

Procedure

The apparatus consisted of two opaque red bowls (15 cm in diameter) separated 40 cm from each other and placed upside down on a 70 × 40 cm wooden plank. A cardboard screen was used to occlude the process by which the experimenter hid the food reward (grapes and orange pieces) under one of the two bowls. For each trial, the experimenter sat behind the apparatus facing the subject and baited one of the two bowls behind the screen. To do this the experimenter placed the screen on the chimpanzee's side of the two bowls, showed the subject a piece of food, dropped the food behind the screen on the center of the platform, dragged both bowls alternately to the center of

the platform, and captured the food reward with one of them. Then the experimenter removed the screen and after making sure that the subject was facing the experimenter and looking at him, the experimenter stared at the correct bowl for 10 s. Staring consisted of orienting the head (and eyes) down and to the side, 45° off the center of the platform so that the experimenter made eye contact with the bowl. After the 10-s period, the experimenter pushed the apparatus forward against the fence (while still staring at the correct bowl), and permitted the subject to select one of the two bowls by touching it. Once subjects had touched a bowl, the experimenter pulled back the apparatus and gave him the contents of the selected bowl. This test consisted of 12 trials administered in a single session. Food location was randomly varied among the two bowls with the only constraint that the reward was never placed in the same bowl for more than 2 consecutive trials. Interobserver reliability was not assessed since subjects' responses (i.e., touching one of the containers) were totally unambiguous.

Results

In this procedure, the chimpanzees as a group failed to choose the correct bowl at above chance levels, $t(5) = 1.19$, $P = 0.14$, one-tailed (Table 2). Subjects were correct, on average, in 6.83 (SD = 1.72) out of 12 trials (56.9%, with a 50% probability of being correct by chance). An analysis of the individual performances indicated that no subject selected the correct bowl at above chance levels either (binomial tests, non-significant in all cases). Finally, there was no evidence suggesting that subjects' performance changed significantly across trials, either when the first six trials were compared to the last six trials (Wilcoxon test: $Z = 0.81$, $P = 0.21$, one-tailed, $n = 6$). However, there seemed to be some evidence of improvement when the first two trials were compared to the last two trials (Wilcoxon test: $Z = 1.73$, $P = 0.04$, one-tailed, $n = 6$).

Discussion

Chimpanzees did not use the human's gaze to select the baited container. This result is comparable to various studies that have shown that capuchin monkeys and rhesus macaques failed to spontaneously use a human's gaze to select the correct container (Anderson et al. 1995, 1996), as well as chimpanzees (Call and Tomasello, 1998) – although both capuchins and chimpanzees can be trained to do so (Itakura and Anderson 1996). Experiment 2 thus provides no support for the hypothesis that chimpanzees understood the experimenter's gaze in a mentalistic manner. The results would thus seem to be consistent with the low-level model in which the subject simply follows the human's gaze until it finds an interesting object. In this case, the bowl by itself was not interesting and so following E's gaze did not lead individuals

to pay special attention to, or behave in special ways towards, the correct bowl.

On the other hand, the current experiment, and others like it, clearly involves more than simple gaze following. To perform successfully the subject must not only follow the human's gaze, but must also make some inference about why the human is looking in the direction he is looking – since there is no obvious target such as food or a predator in sight. Indeed, one might ask whether it is reasonable at all for a human to be looking at an opaque container with no food in sight. It would not seem to be a natural behavior. In the next two studies, therefore, we arranged things so that the human could see the food – so it was natural that he should be looking at it – while the chimpanzee subjects could not because of two different kinds of barriers blocking their view. Thus, again human gaze direction was their only cue, but in this case the context in which the human performed his looking behavior was more meaningful.

Experiment 3

In this experiment, as in the previous experiment, we investigated whether chimpanzees were able to use E's direction of gaze (head and eye orientation) to select the one container (out of two) with food. In this case, however, the containers were tubes which could be peered into both from E's side and from the subject's side. The tubes had a barrier inside them so that E, but not the chimpanzee, could see the food resting in his side of the tube. We also presented trials using the pair of bowls from the previous experiment to assess the possibility of learning across trials and experiments.

Method

Subjects

The subjects were the same as in experiment 1.

Procedure

The apparatus consisted of the two opaque red bowls and the wooden plank used in the previous experiment, and two opaque white "tubes" square in section (5 × 5 × 30 cm). Each of these tubes was fitted with a square piece of cardboard inside the tube at about 5 cm from one of its ends that prevented subjects from seeing through it. In addition, this cardboard piece created a 5-cm container on that end of the tube permitting the experimenter to hide a piece of food there without the subject seeing it. A pair of either bowls or tubes was placed on the wooden plank in different trials. As before, the bowls or the tubes were separated by 40 cm and a cardboard screen was used to occlude the hiding process from the subject.

Before testing began subjects were given the opportunity to explore and manipulate the tubes through the fence. Subjects explored the tubes in various ways such as looking through them, touching them, and poking the cardboard piece inside the tubes with their fingers. No familiarization procedure was used with the bowls because subjects had manipulated them in the previous experiment. Testing began after the tube habituation, which lasted from less than a minute to 10 min depending on the subjects' interest.

The testing procedure was almost identical to the one used in experiment 2. The only difference was that there were two types of trials, depending on the type of container used. In the bowl trials, the experimenter followed exactly the same procedure as in experiment 2. That is, the experimenter sat behind the apparatus facing the ape and baited one of the containers from behind a screen, stared at the correct container, removed the screen, continued to stare at the container for another 10 s, and finally gave the subject a choice by pushing the apparatus against the fence. In the tube trials, the experimenter used the pair of tubes situated on each side of the platform and oriented perpendicular to the fencing, with the ends of the tubes that contained the cardboard piece situated closer to E's location. The baiting process was conducted in the following manner. The experimenter placed the screen in front of the tubes, moved the tubes to the center of the platform, showed a piece of food to the subject, and placed it inside one of the tubes on the side with the cardboard piece (on each trial he placed his hand inside both tubes but put the reward inside only one of them). After the subject was attending, E moved each tube to its original position (perpendicular to the fence), stared at the food inside the tube, removed the screen, and continued to stare at the food for 10 s. From where E was seated, he (but not the subject) was able to see the food inside the tube. After this 10-s period, E pushed the apparatus forward against the fence (while still looking at the correct tube), and permitted the subject to select one of the two tubes.

The test consisted of a total of 24 trials administered in two sessions. Each session consisted of a series of six bowl and six tube trials presented alternately. Half of the subjects started their respective series with a bowl trial while the other half of the subjects started their series with a tube trial. Food location was randomly varied among the two containers with the constraint that the reward was never placed in the same container for more than two consecutive trials.

Results

Subjects selected the correct tube at a rate significantly above chance, $t(5) = 4.57$, $P < 0.005$, one-tailed (Table 2). They chose the correct tube an average of 9.67 (SD = 1.97) times out of 12 trials (80.6%, chance = 50%). In contrast, the subjects failed to choose the correct bowl at above-chance levels $t(5) = 1.51$, $P = 0.09$, one-tailed.

They chose the correct bowl an average of 7.33 (SD = 2.16) times out of 12 trials (61.1%, chance = 50%). A direct comparison between the two types of trials revealed that subjects were significantly more successful in the tube than in the bowl condition (Wilcoxon test: $Z = 2.02$, $P < 0.05$ one-tailed, $n = 6$). Analysis of individual performances revealed that four of six subjects in the tube condition, but only one subject in the bowl condition, selected the correct container at above chance levels (binomial tests, $P < 0.05$).

There was no evidence suggesting that subjects significantly improved across trials in either of the two types of trials, either when the first six trials were compared to the last six trials (Wilcoxon tests; bowl: $Z = 1.34$, $P = 0.09$, one-tailed; tube: $Z = 0.38$, $P = 0.35$, one-tailed; $n = 6$ in both cases), or when the first two trials were compared to the last two trials (Wilcoxon tests; bowl: $Z = 1.00$, $P = 0.16$, one-tailed; tube: $Z = 1.34$, $P = 0.09$, one-tailed; $n = 6$ in both cases).

Discussion

Chimpanzees used E's gaze direction to select the baited tube, but still did not use E's gaze direction to select the baited bowl. Given that the trials with bowl and tube were alternated in the same testing session, the difference between conditions cannot be attributed to practice effects. Since E's looking behavior was identical in the two conditions, the nature of the container would seem to be the only difference that could have caused the difference in subjects' performance in the two conditions.

Although the bowls and tubes differ from one another in several ways, there are two ways that seem especially important in the current context: (1) E could see the food, and (2) the subject could look inside its side of the tube (even though the food was not visible from that side). The point would seem to be that from their previous experience with tubes – both in their natural lives (some of the individuals had had experience with both small tubes and large concrete conduits inside which they played) and during the exploration and manipulation phase prior to testing in the current experiment – the chimpanzees in this experiment knew something about how the gaze direction of others might work with tubes. Thus, if we invoke the low-level model of primate gaze following, in the tube condition of this experiment the subject would have followed E's gaze, would have seen a particular tube, perhaps would have looked inside the tube, but then would have seen nothing interesting (assuming that the tubes were no more inherently interesting than the bowls).

It would thus seem that the low-level model is not sufficient to account for the chimpanzees' behavior in this condition, since they chose the tube E looked at even though they themselves saw nothing of particular interest when they followed E's gaze. One possibility is that they understood that E could see the food even though they could not – thus making E's look meaningful in a way that it was not in the bowl condition in which neither E nor the

subject could see food. To explore this possibility further, we performed the same basic experiment again, but in this case used another kind of barrier in which E could see the food but the subject could not.

Experiment 4

In this experiment we used exactly the same procedure as in Experiment 3 except that we substituted barriers for tubes. That is, in this case there was a piece of plastic that was placed so that E could see the food while the subject could not. In general, it might be assumed that barriers constitute a more challenging obstacle than tubes because an individual cannot look inside a barrier from its own side as in the case of a tube; to see what is behind a barrier normally requires moving to a position on the other side. Again, trials using the pair of bowls from the previous experiment were used to directly compare the subjects' performance with the barrier condition and to assess the possibility of learning across trials.

Method

Subjects

The subjects were the same as in experiment 1.

Procedure

The apparatus consisted of the two opaque red bowls and the wooden plank used in the previous experiment, and two self-supported opaque white barriers (25 × 15 cm). Each of these barriers was formed by joining two container bins of the type used to store small items such as nuts and bolts. These barriers prevented subjects from seeing objects located behind them. The occluders were placed on the platform separated by 40 cm, and food was hidden with the help of the cardboard screen used in previous experiments.

Before testing began subjects were given the opportunity to explore the perceptual features of the barriers. In particular, subjects were shown both sides of the barrier and the possibility of seeing hidden food when the barrier was rotated. Thus, E baited one the barriers behind the screen, and then turned the platform around 180°. After subjects had observed the location of the food, E turned the platform around by 180° again and let subjects choose one of the barriers. Subjects received a series of 12 trials of this type in a single session. Most subjects correctly selected the baited barrier on most trials. The testing procedure was identical to the one used in the previous experiment, with the only difference that barriers were used instead of tubes.

Results

Subjects selected the correct barrier at a rate significantly above chance, $t(5) = 5.40$, $P < 0.005$, one-tailed (Table 2). They chose the correct barrier an average of 8.17 (SD = 0.98) times out of 12 trials (68.1%, chance = 50%). In contrast, subjects failed to choose the correct bowl at above-chance levels $t(5) = 0.60$, $P = 0.29$, one-tailed. They chose the correct bowl an average of 6.67 (SD = 2.73) times out of 12 trials (55.6%, chance = 50%). Analysis of individual performances revealed that no subject in the barrier condition (binomial tests, $P > 0.05$ in all cases) – and only one subject in the bowl condition (binomial test, $P < 0.05$) – selected the correct container at above chance levels.

A direct comparison between the two types of trials revealed that subjects were not significantly more successful in the barrier than in the bowl condition (Wilcoxon test: $Z = 1.16$, $P = 0.13$, one-tailed, $n = 6$). However, subjects' performance changed across trials such that they performed at a higher level in the first six trials than in the second six trials in the barrier condition (Wilcoxon test: $Z = 2.24$, $P < 0.02$, one-tailed, $n = 6$) but not in the bowl condition (Wilcoxon test: $Z = 1.00$, $P = 0.16$, one-tailed, $n = 6$). A re-analysis of the direct comparison between bowl and barrier trials using only the first set of six trials indicated that subjects were significantly more successful in the barrier than in the bowl condition (Wilcoxon test: $Z = 1.81$, $P < 0.05$ one-tailed, $n = 6$).

Discussion

Although their performance was somewhat weaker than with the tubes in experiment 3, as a group the chimpanzees in experiment 4 performed at above chance levels with the barriers (but continued to perform at chance with the bowls). Again, given that the trials with bowl and barrier alternated in the same testing session and that E's behavior was the same in both conditions, the differences observed between conditions were most likely due to the nature of the containers and the subjects' understanding of them. The chimpanzees in this experiment had had previous experience with barriers – both in their natural lives in various captive settings and in the habituation period of this experiment – and so it seems that they had come to know something about how the gaze direction of others might work with barriers.

Thus, once again, it would seem that the low-level model of primate gaze following is not sufficient to account for the chimpanzees' behavior with the barriers, since they chose the tube E looked at even though they themselves saw nothing of particular interest when they followed E's gaze. Again, one possibility is that they understood that E could see the food even though they could not – thus making E's look meaningful in a way that it was not in the bowl condition. In a general way these findings are consistent with those of Povinelli and Eddy (1996), who found that chimpanzees often looked around

a barrier to see what the human was looking at on the side away from them.

Combining results of experiments 3 and 4

Because the tubes and barriers from experiments 3 and 4 allowed E to see the food, whereas the bowls in these same studies did not, we also did a combined analysis in which subjects' performance was tallied for the 24 trials in which they saw either tubes or barriers, and these were then compared to the 24 trials in which they saw only bowls (numbers for each individual can be computed from Table 2). The mean score for the tubes+barriers condition was 17.83 (SD = 1.94), whereas for the bowls it was 14.00 (SD = 3.95), $t(5) = 3.0$, $P < 0.02$, one-tailed. In this combined analysis, five of the six subjects were above chance in the tubes+barriers condition (17/24 or above, one-tailed binomial test), whereas only two of the six subjects were above chance in the bowls condition. Comparison of the tubes and the barriers showed no significant difference ($t(5) = 1.51$, $P = 0.19$, one-tailed), although more subjects were above chance as individuals in the tube condition (four) than in the barriers condition (none).

Since the chimpanzees used in these experiments showed marked inter-individual differences, we decided to investigate the possible source of these differences by exploring the effect of age and rearing history on the scores for both bowl and tube+barrier conditions. Based on the review of the literature by Call and Tomasello (1996), it was predicted that older subjects would perform better than younger ones, and that chimpanzees with extensive human contact (i.e., Peony and Ericka) would perform better than the other chimpanzees included in this experiment. Contrary to our predictions, no significant effect of age was found either in the bowl (Spearman $r = 0.03$, $P = 0.96$, $n = 6$) or the tube+barrier condition (Spearman $r = 0.35$, $P = 0.49$, $n = 6$) although this could be attributed to the fact that all subjects included in the experiment were adults. A quadratic function also failed to fit the observed values in the tube+barrier condition ($F = 4.22$, $df = 3$, $P = 0.13$). Similarly, rearing history did not affect the score in the bowl condition (Mann-Whitney test: $Z = 1.17$, $P = 0.12$, one-tailed, $n = 6$), even though chimpanzees with extensive human contact as a group scored higher than the rest of the chimpanzees (mean = 17.0, SD = 1.41; mean = 12.5, SD = 4.04, respectively). In contrast, rearing history did have a significant effect in the tube+barrier condition (Mann-Whitney test: $Z = 1.91$, $P < 0.05$, one-tailed, $n = 6$). Chimpanzees with extensive human contact scored higher (mean = 20.0, SD = 0) than the rest of chimpanzees in this experiment (mean = 16.75, SD = 1.26).

General discussion

Chimpanzees followed the gaze of a human experimenter to an external location and checked back to the human's

face when they did not find anything interesting or unusual (experiment 1). This behavior was quite robust as all six individuals engaged in this behavior, and the chances of looking in that specific direction outside the context of another's gaze was shown to be quite low. In an object-choice task, chimpanzees also used the human's gaze direction to choose the tube or barrier containing food (experiments 3 and 4). However, they did not use the human's gaze to decide between opaque bowls (experiments 2, 3, and 4). Given that the human's gaze was the only source of information on the location of food in experiments 2–4, the subjects' superior performance with tubes and barriers, as compared with bowls, would seem to have something to do with differences in the occluders and what they meant for individuals' understanding of the situation facing them.

There are at least four hypotheses invoking different levels of cognitive sophistication that may explain the mechanism used in our choice situation: orientation, orientation combined with differential foraging tendencies, understanding of seeing in others, and understanding of seeing and knowing in others. The first two hypotheses correspond to low-level cognitive mechanisms, whereas the last two hypotheses represent higher-level cognitive mechanisms involving the understanding of the psychological states of others.

First, the orientation hypothesis predicts that subjects are preferentially attracted to the occluder that the experimenter is looking at, in the same way that they would be attracted to an occluder touched by the experimenter (i.e., stimulus enhancement). Thus, this hypothesis predicts that for all three occluders (bowls, tubes, and barriers) subjects should simply follow the human's gaze and select the one he was staring at. This hypothesis, however, can be rejected because subjects failed to find the food in the bowl condition.

Second, although a simple orientation explanation is not sufficient to account for the chimpanzees' choice behavior, it is possible that orientation may still work when paired with some chimpanzee differential foraging tendencies. One possibility is that the upside-down bowl it is not very important to subjects in the context of foraging in their typical captive environment. On the other hand, our subjects presumably have had many experiences in which they have discovered food behind barriers (e.g., screens, walls). Similarly, although tubes are fairly specialized objects, both wild and captive chimpanzees are very interested in holes and often look into them and poke things into them – usually in search of food. Indeed, many of our subjects had had experience with artificially constructed foraging boxes (with holes into which they could poke sticks for honey) in their outdoor areas. So this second hypothesis is that our chimpanzees, either naturally or on the basis of some experiences specific to them, believed that barriers and tubes (holes) are good places to search for food, whereas upside-down bowls are not. Thus, after they followed the experimenter's gaze to a bowl, they had no tendency to search there and so they just picked randomly. In contrast, after they followed the experimenter's gaze to a barrier or a tube, they often picked that one be-

cause they knew that food is often found in those kinds of places. This second hypothesis, however, is weakened by the fact that five of the six chimpanzees in this study had found food under various types of opaque containers for several hundreds of trials in previous experiments (e.g., Call and Tomasello, 1998, in press; Tomasello et al. 1997).

Although subjects did not perform significantly better in the tube than in the barrier condition, there was a tendency towards better performance in the tube condition (four individuals were above chance in the tube condition compared with none in the barrier condition). According to this second hypothesis, this finding would be explained by a stronger tendency to search for food in tube-like or hole-like spaces than behind barriers. Therefore, orientation paired with a previous interest in barriers or tubes, may explain our results. Note that this explanation is not a cognitively complex one because it is based on mere orientation response superimposed onto foraging tendencies. This same explanation can also be applied to the findings of Povinelli and Eddy (1996) that some chimpanzees attempted to look to a human's side of a barrier in her visual line of regard; that is, the individuals in this case followed her gaze until they encountered a place where food might be located and then they looked there.

The third hypothesis embraces a higher-level cognitive account of the chimpanzees' behavior and involves some level of understanding of seeing in others rather than a simple combination of orientation responses supplemented by foraging tendencies. There is a weak and a strong version of this hypothesis corresponding roughly to the distinction between level 1 and level 2 in visual perspective taking (Flavell 1985, 1992). The weak version involves understanding that others can see things that the subject herself cannot see. Chimpanzees might know that the gaze behavior of others has a different significance in different situations. For example, chimpanzees must experience many social situations in which they: (1) notice and follow the gaze direction of another individual, (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 the individual moves around the barrier. Subjects in the current study have certainly experienced these situations because barriers of several types, including tube-like structures, are present in their enclosures. They have thus had the opportunity to discover the significance of others' gaze in various situations of occlusion, and so this explanation is in effect that chimpanzees use the gaze of others as a social cue and they have learned several variations as to how this cue works in different situations. Their excellent performance with the tube specifically in the current study does not fit well with this explanation. However, as the chimpanzees' experience with tubes, although not formally tested, is certainly less than with barriers in general, since barrier-like structures such as walls, doors, or poles are more common and varied in the chimpanzee enclosures than tube-like structures (e.g., barrels).

On the other hand, the strong version of understanding of seeing in others not only involves knowing that others may see things that the subject is not capable of perceiv-

ing at the moment (due to occlusion), but also appreciating that others can have different views of the same object. That is, not only do subjects have an expectation that something might be behind a barrier because a conspecific is looking behind it (weak version), but also they may imagine how they would see it if they were in their conspecific's place (i.e., perspective taking). Unlike the weak version of understanding of seeing in others, this stronger version may explain why subjects tended to perform better with tubes than with barriers. The reason is that looking through an unblocked tube gives the subject good information about what another individual looking through the other side of the tube sees. In contrast, in the barrier situation the subject cannot directly see what another individual sees unless she moves around the barrier or the orientation of the barrier is changed – which was not possible in the current study.

Finally, the fourth hypothesis involves the highest level of social-cognitive functioning, invoking concepts such as knowledge in others and the relation between seeing and knowing in others. This hypothesis predicts that chimpanzees would be able to select the correct occluder regardless of its type because when the experimenter hid the food, he *saw* its hiding place, and consequently, he *knew* where the food was located. In this context, chimpanzees would have interpreted the experimenter's gaze as a useful guide to locating the food in all three conditions because they would have understood that the experimenter knew where the food was located. This hypothesis can be rejected on the basis of the current results because subjects failed to use the experimenter's gaze direction as a guide in the bowl condition, even though subjects watched the experimenter hide the food, so they might easily have inferred that the experimenter watched the hiding process (indeed did the hiding), and so he knew where the food was. Thus, chimpanzees did not show an understanding that seeing leads to knowing. These findings are consistent with what we know about chimpanzee social cognition in general. For example, in a different type of object-choice task, Povinelli et al. (1990) found that for many scores of trials their four chimpanzees did not reliably choose the human who had watched a hiding process as their informant (as opposed to one who had not watched it) and performed at chance levels in their initial transfer trials (Povinelli 1994).

Alternatively, it is possible that chimpanzees know about knowing in others and that our experimental setup in the bowl condition did not help subjects to establish a good seeing-knowing connection because the experimenter's seeing (which took place during the baiting) was not clear enough; and the experimenter staring at an opaque bowl after the baiting process did not help either. It would be interesting to have an experimental condition in which the experimenter hid the food, then looked at the contents of the two bowls in front of the subject by lifting them up and closing each one in succession, stared at the correct one, and gave the subject a choice.

There is a growing body of evidence suggesting that apes raised by humans tend to outperform other apes in a

number of socio-cognitive domains such as imitative learning (Hayes and Hayes 1952; Tomasello et al. 1993), joint visual attention (Carpenter et al. 1995), gestural communication (Call and Tomasello 1994, 1996; Gómez 1996), and distinguishing intentional from accidental actions in others (Call and Tomasello 1998). Thus, differential rearing histories could also explain some of the inter-individual differences found in this study, in which chimpanzees with extensive human contact also outperformed chimpanzees with less human contact. However, the mechanism responsible for these differences remains unclear. One possible explanation for these differences may be the experimental situation, and more specifically the presence of a human experimenter. For instance, chimpanzees raised by humans may have paid more attention to the experimenter, read the experimenter's behavior more easily, or simply be more comfortable and less prone to distraction in the experimenter's presence. During testing, however, there was no indication (as far as we could ascertain) that one group of chimpanzees was less comfortable with the experimental situation than the other. Alternatively, differences between chimpanzees in this study may be because chimpanzees with extensive human contact could have developed a better understanding of the process of seeing in humans than chimpanzees with less human contact. This idea is supported to some extent by this study because the differences between groups of chimpanzees were mainly observed when food was visible to the experimenter. Although the evidence is suggestive, at this point it is still not possible to decide between the various alternatives and future studies should attempt to investigate the specific effects of human enculturation on the cognitive abilities of primates.

The current study was different from previous studies in that the experimenter's visual access to the food continued in all conditions while subjects were choosing, whereas in other studies (e.g., Povinelli et al. 1990) the experimenter's looking at the food in its hiding place took place some seconds before the subject's choice. It is therefore possible that seeing leads to knowing only when subjects see that the experimenter is seeing (thus knowing), but not if they have to recall the seeing event that took place some seconds before the subject's choice. If this "simultaneous seeing-choosing" explanation were correct, subjects would fail in the barrier and tube conditions after introducing a delay between the experimenter seeing and the subject's choice. For instance, the experimenter could stare at the correct barrier or tube (as in the current study), then look at the subject for a certain period of time, and finally give him or her a choice. To solve this problem, subjects would have to recall which occluder the experimenter stared at before he looked at them. Passing this test, however, would not necessarily mean that subjects understood knowledge states in others, because they could have simply remembered what occluder the experimenter was oriented to. Ultimately, the problem with this simultaneous seeing-choosing explanation is that seeing becomes inseparable from knowing since subjects need to observe the experimenter seeing while they choose in or-

der to infer the experimenter's knowledge states. Under these circumstances, however, there is no need to invoke the experimenter's knowledge states at all, and the third hypothesis discussed previously would suffice.

The finding that subjects used the experimenter's signals only when he was able to see the food is important and may have considerable repercussions for the way we study the comprehension of signals in locating food in primates. Invariably, all studies have used opaque occluders to hide food and the experimenter has used a signal to indicate its location to subjects (Anderson et al. 1995, 1996; Mitchell and Anderson 1997; Call and Tomasello 1994; Woodruff and Premack 1979; Tomasello et al. 1997; Povinelli et al. 1990, 1991). Under those circumstances, most studies report that primates fail (or slowly learn) to select the designated occluders. An intriguing possibility that deserves future research attention is that if the occluders had permitted the experimenter to see their contents (as in the tube or the barrier condition) the signals might have been more easily interpreted by subjects.

In summary, our findings allowed us to discard the simple hypotheses of orientation and understanding seeing-knowing in others that have been proposed to explain gaze following in chimpanzees in an object-choice situation. However, they did not allow us to conclusively choose between the hypotheses of orientation combined with foraging tendencies and understanding seeing in others, or between the weak and the strong interpretations of this last hypothesis. Our own inclination is to remain cautious until convergent data from other studies help to disambiguate these findings. One interesting possibility raised by the current results is that chimpanzees might show their most sophisticated social cognitive skills in situations in which the behavior of another (e.g., looking behavior and seeing) is happening concurrently with their own decision-making process. Thus, studies in which the human cannot see the reward at the time of subject choice because it is in an opaque occluder may potentially be underestimating primates' social knowledge. In either case, this study provides new information about chimpanzee gaze following that should help us to further specify the cognitive mechanisms underlying this important social behavior.

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