

REPORT

Chimpanzee use of human and conspecific social cues to locate hidden food

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Abstract

Two studies are reported in which chimpanzees attempted to use social cues to locate hidden food in one of two possible hiding places. In the first study four chimpanzees were exposed to a local enhancement cue (the informant approached and looked to the location where food was hidden and then remained beside it) and a gaze/point cue (the informant gazed and manually pointed towards the location where the food was hidden). Each cue was given by both a human informant and a chimpanzee informant. In the second study 12 chimpanzees were exposed to a gaze direction cue in combination with a vocal cue (the human informant gazed to the hiding location and produced one of two different vocalizations: a 'food-bark' or a human word-form). The results were: (i) all subjects were quite skillful with the local enhancement cue, no matter who produced it; (ii) few subjects were skillful with the gaze/point cue, no matter who produced it (most of these being individuals who had been raised in infancy by humans); and (iii) most subjects were skillful when the human gazed and vocalized at the hiding place, with little difference between the two types of vocal cue. Findings are discussed in terms of chimpanzees' apparent need for additional cues, over and above gaze direction cues, to indicate the presence of food.

The ability to follow the gaze direction of conspecifics to outside objects and events would seem to be a social skill with immediate adaptive benefits for a wide range of animal species. For primates, it would seem to be especially useful for such things as discovering predators, locating food and monitoring important social events in the group. In addition, a number of theorists concerned primarily with human social cognition have posited that the monitoring of eyes and the following of gaze direction are important phylogenetic building blocks in the evolution of a human-like 'theory of mind' (e.g. Baron-Cohen, 1995).

Recently, there have been a number of studies of nonhuman primates' ability to use gaze direction and other social cues, such as the human pointing gesture, to locate outside entities. The findings are decidedly mixed and seem to depend on the experimental paradigm employed. There are two basic paradigms. The first is simple gaze following in which one individual orients its head and eyes in a certain direction, sometimes accompanied by gestures, and another individual either

does or does not orient similarly as a result. For example, Itakura (1996) approached primate individuals and either looked, or looked and manually pointed, to the right or left. Many individuals of the 11 primate species tested visually tracked the pointing gesture, but only one (an orangutan) visually followed gaze direction by itself. Using a similar methodology, Povinelli and Eddy (1996) found that six juvenile chimpanzees also followed human gaze direction, without a pointing gesture. In the one experimental study in which primates were asked to follow the gaze of conspecifics in a social group setting, Tomasello, Call and Hare (1998) found that all five species tested followed conspecific gaze very skillfully. Since some of these species were the same as, or very closely related to, those who did not follow human gaze in the study of Itakura (1996), it is possible that many nonhuman primates find it more natural to follow the gaze of conspecifics than that of humans.

The other experimental paradigm involves an informant looking to (or pointing and looking to) the location of food hidden under one of several opaque

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containers: the so-called object choice paradigm. Perhaps surprisingly, in this paradigm there are no clear cases of success in nonhuman primates. Anderson, Sallaberry and Barbier (1995) found that capuchin monkeys did not use human gaze direction to find food in this task, the only effective cue being when the human placed his hand directly next to the baited container. Itakura and Anderson (1996) trained a single capuchin monkey to follow human eye gaze to hidden food in a similar situation, but it took them over 120 trials to do so, suggesting the possibility that gaze direction was learned as a straightforward discriminative cue. Tomasello, Call and Gluckman (1997) found that chimpanzees and orangutans did not use a distal human pointing gesture, without a gaze direction cue, to locate food in a similar object choice procedure, and Call, Hare and Tomasello (in press) found negative results when chimpanzees were given simple gaze direction cues, with no other gestures, in this same experimental paradigm. (No study with chimpanzees has used a pointing gesture and a gaze cue together in this paradigm.) Povinelli, Bierschwale and Cech (in press) found that some chimpanzees could use gaze direction cues in this paradigm, but a variety of lines of evidence led to the interpretation that the subjects were using gaze as a simple discriminative cue (see also Itakura & Tanaka, 1998). Interestingly, however, Call *et al.* (in press) found positive results when they used as the hiding place a special kind of tube – which might by itself suggest food to the chimpanzees since they naturally look for food in holes. In a slightly different experimental paradigm, Povinelli and Eddy (1997) found that a head-bobbing gesture helped chimpanzees to make effective food-relevant choices as well.

One possible explanation for the poor performance of chimpanzees and other primates in using simple gaze cues in the object choice paradigm is that the informant in all of the studies was a human being. Just as a number of primate species find it easier to follow conspecific than human gaze in the gaze following paradigm, so too they might find it easier to follow conspecific than human gaze in the object choice paradigm. A second possible explanation is that a simple gaze cue by itself is not enough to suggest the presence of food in the gazed-at location. Thus, the only positive finding in the object choice paradigm involved a situation in which the subject had information other than gaze direction that food may be found in the gazed-at location (Povinelli & Eddy, 1997; Call *et al.*, in press).

In the current two studies we sought to test both of these possible explanations. First, in an initial study we compared the performance of chimpanzees in an object choice task when the social cue was given by a human

informant and by a chimpanzee informant. Second, also in this initial study, on different occasions each of these two species of informant gave one of two different cues: a local enhancement cue in which they approached and then remained beside the baited container (as they might do to initiate a real foraging situation when food was discovered) and a gaze/point cue in which they simply looked at and pointed to the baited container (no other study in this paradigm has used gazing and pointing together for chimpanzees). Following along these lines, in a second study a human informant attempted to indicate the location of food for the chimpanzee subjects by gazing at the baited container (using no other gestures) and vocalizing in one of two different ways (no other study in this paradigm has used gazing and vocalizing together for any primate species).

Study 1

The purpose of this study was to compare chimpanzees' ability to use two different social cues to object location in an object choice paradigm, each provided by both a human informant and a conspecific informant (for a total of four different cues). For the local enhancement cue the informant approached and looked at the location where food was hidden and then remained beside it. For the gaze/point cue the informant stood equidistant between the two hiding locations, and then turned his head, gazed, and manually 'pointed' towards the baited location.

Method

Subjects

Four adult chimpanzees (*Pan troglodytes*) served as subjects (Jessie, Travis, Barbara, Cissie). Two additional adult chimpanzees from a different group served as informants (Erika, Vivian – Erika near the top of her dominance hierarchy and Vivian near the bottom). All subjects and informants were housed at the Yerkes Regional Primate Research Center Field Station in small group cages with indoor and outdoor areas. Testing took place in the indoor areas. Animals were fed on their normal schedule throughout all phases of testing.

Materials and design

Each subject was individually tested for its ability to follow social cues to food (fruit) hidden under one of two opaque containers (12 cm × 7 cm × 7 cm) placed on a wooden board 2 m apart (the apparatus). The chimpanzee informant was located in a cage directly

across a hallway from the subject, approximately 3 m away. When a chimpanzee was informant, the apparatus was placed in front of her cage, she gave her cue, and then an experimenter slid the apparatus across the hall so that the subject could make its choice. The human informant interacted with subjects from the hallway. He gave his cue from immediately behind the apparatus in the hallway area, and again after the cue was given the apparatus was slid up to the subject's cage so that its choice could be made. Figure 1 depicts the spatial layout of the experiment.

There were four different types of experimental trials, resulting from the factorial combination of two dimensions. First was the type of informant: human or conspecific. Second was type of cue: local enhancement or gaze/point. Each subject participated in 24 experimental trials in each of these four conditions, with each condition run as a block, for a total of 96 trials per subject. Subjects were also given an additional 24 trials in the conspecific local enhancement condition with a second conspecific informant – just as an additional check. Conditions were administered in the order:

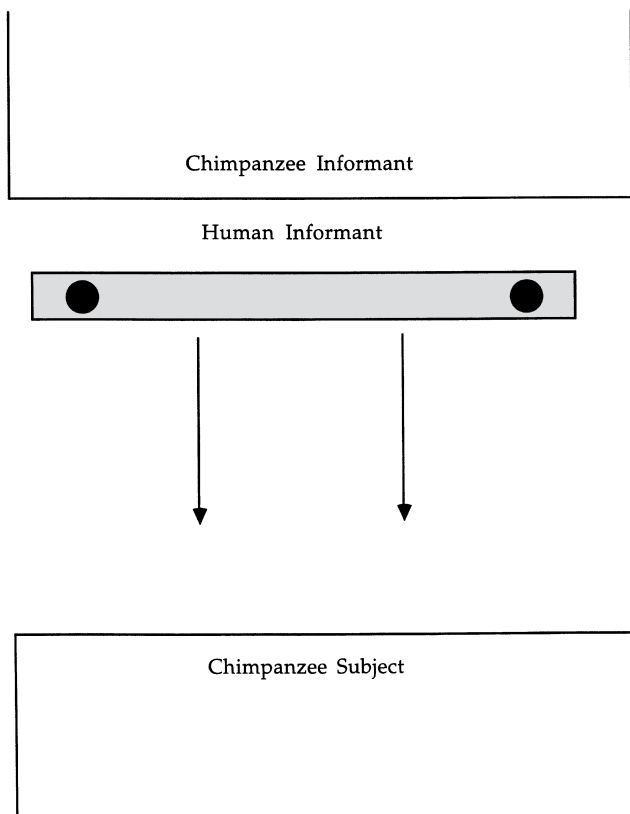


Figure 1 *Experimental arrangement for Study 1. For Study 2, the human informant was closer to the subject's cage and the apparatus was smaller.*

conspecific local enhancement, conspecific gaze/point, human local enhancement, human gaze/point. (Counterbalancing order of conditions was not possible because the training of chimpanzee informants had to go in a specific order – see below.) All trials for a given subject were administered within a 1 month period, with daily sessions comprising no more than 24 trials. Food placement was randomized so that each container was baited an equal number of times in each experimental condition for each subject, with the same container never baited three times in a row.

Procedure

All of the subjects had participated in previous experiments, and so the pre-training necessary to prepare them for the experiment was minimal. For each subject's pre-training, an experimenter in the hallway sat behind the apparatus, placed food in one of the containers in full view of the subject, and then slid the apparatus flush against the subject's cage. Based on their training from previous experiments, the subjects then knew to choose one (and only one) of the containers by bodily moving to it and touching it through the caging. Each of the four subjects was given approximately ten pre-training trials of this type before testing began. All subjects chose correctly on virtually all of these pre-training trials.

Training of the chimpanzee informants was more extensive. The two chimpanzee informants, Erika and Vivian, were first individually trained to give the local enhancement cue. Holes were cut out of the backs of the two containers so that they could see the food inside from their viewing angle. When they approached the container with food and stayed beside it (typically looking at the food, but almost never vocalizing – vocalizations occurred on a total of three experimental trials) they were rewarded. Erika was trained first, and then subjects were individually run with her as informant. Then Vivian was trained and subjects were run with her as informant. After this, Erika was also trained to give the gaze/point cue (Vivian could not be trained to give this cue). For this cue, Erika sat equidistant between the two containers and simply looked towards the food, which again she could see through the hole in her side of the container. As an infant Erika had been raised in a human home, and later was given further human training, so she spontaneously 'pointed' to food in this situation – arm and index finger extension towards the food (ipsilateral arm). The trials with human informants followed upon the completion of all of the trials with the chimpanzee informants, and they were patterned as closely as possible on those trials. For the local enhancement cue the human approached

the baited container and squatted beside it, looking alternately to it and the subject. For the gaze/point cue, the human stood equidistant from the two containers and pointed and looked at the baited container (ipsilateral arm). It should be noted that the local enhancement cue was intended to resemble in broad outline what individuals might do to initiate a real foraging situation when they discovered food: approach it, look at it, remain near it.

The procedure by which all four types of experimental trials were administered was basically the same. From the hallway, an experimenter raised a cardboard screen on the subject's side of the apparatus (approximately 3 m × 1 m) so that subjects could not see the apparatus or the hiding process (although they could see the experimenter's movements from the waist up). The experimenter then baited one container and sham baited the other. For conspecific informant trials, the apparatus was then pushed flush to the informant's cage so that the cue could be given. For human informant trials, the apparatus was moved slightly and then the human informant took up his position and gave his cue. For both types of informants the cue was given for approximately 5 s after the time that the subject clearly looked at the informant (as determined by agreement of the two humans present). The apparatus was then pushed over to the subject so that a choice could be made.

Scoring

A subject's choice for a given trial was the first container it touched. Responses were totally unambiguous (and subjects searched on every trial), so the two experimenters simply noted independently after each trial which container the subject had chosen. Agreement between the two experimenters was 100%.

Results

Performance for each subject in each experimental condition is presented in Table 1. The most straightfor-

ward data analysis compared the number correct against chance, for each subject for each of the four experimental conditions separately. Given a 50% chance probability, 17/24 correct was greater than would be expected by chance ($p < 0.05$, one-tailed binomial probability). Results of this analysis showed that, for conspecific local enhance all four subjects were above chance; for human local enhance three subjects were above chance; for conspecific gaze/point no subject was above chance; and for human gaze/point one subject was above chance.

To assess the relative effectiveness of the four different types of social cue, a two-way analysis of variance (ANOVA) was run with Type of informant (human, conspecific) and Type of cue (local enhance, gaze/point) as variables. The one significant finding was that the local enhance cue was more effective than the gaze/point cue regardless of informant, $F(1, 3) = 14.31$, $p < 0.01$. There was no effect of Type of informant and no interaction between the two variables.

Patterns of individual performance were relatively consistent across the four subjects. Two subjects were good in the two local enhancement cues only, with one additional subject being good when the local enhancement cue was given by a conspecific only. The fourth subject, Travis, was good on the two local enhancement cues also, but in addition he was above chance on the gaze/point cue when it was given by the human. Interestingly, in the latter condition Travis was at chance for the first 13 trials (7/13 correct), but then was nearly perfect for the last 11 trials (10/11 correct). This suggests that Travis did not come to the experiment knowing how to use this cue, but rather that he learned it during the course of the experiment. In terms of patterns of errors, when Cissie did not know where the food was located she showed a marked side bias, choosing the right side more than twice as often as the left side. When Barbara and Jessie did not know where the food was located, they chose the container that had contained the food on the immediately preceding trial about 70% of the time. Travis's errors were basically random.

Table 1 Number correct, out of 24, by each subject in each experimental condition in Study 1

	Conspecific local enhance	Conspecific gaze/point	Human local enhance	Human gaze/point
Travis	20* (18)*	13	18*	17*
Cissie	19* (18)*	15	20*	10
Jesse	18* (21)*	13	17*	11
Barbara	17* (18)*	13	12	12
Average	18.63	13.50	16.75	12.50

Notes: Numbers in parentheses are re-test with second conspecific informant.
* $p < 0.05$, binomial probability.

Discussion

Perhaps the most important finding of the current study was that the species of informant did not make a difference in chimpanzees' performance. With the local enhancement cue there was a slight advantage for the chimpanzee informant (four to three subjects above chance), but with the gaze/point cue the slight advantage was in the opposite direction (one subject above chance with the human informant only). Obviously this does not mean that just any species will do. The great physical and social similarity of humans and chimpanzees presumably makes their substitution for one another feasible in this situation, and, in addition, all of the subjects in the current study had had daily contact with humans (albeit mostly of a fairly superficial nature) basically throughout their lives. But the current findings do provide some validation that studies of chimpanzee (and perhaps other primate) gaze following using human informants may indeed be representative of those individuals' social skills with conspecifics as well – at least in some situations.

The second important finding was that the local enhancement cue seemed to be informative for the chimpanzee subjects, whereas the gaze/point cue did not. All of the subjects were good in using the local enhancement cue with two chimpanzee informants and one human informant. On the other hand, only one subject used the gaze/point cue effectively, and he did so only with the human informant and only beginning on trial number 14 in that session (and he had earlier experienced 24 gaze/point trials with the conspecific informant, each with feedback). To account for this difference in effectiveness of the two types of cue, it is reasonable to consider the possibility of an order effect since, for logistic reasons, we were unable to counter-balance the order in which subjects experienced the cues. But it may be pointed out that the most obvious direction for an order effect would be an advantage for the cue run second because by this time subjects would have had more trials (each with feedback about correctness) in which to learn gaze direction (present in all cues) as an effective cue. But in fact the gaze/point trials were run second for all subjects with both informants, and they were clearly more difficult for subjects. (And fatigue or flagging motivation were not allowed to be important factors as subjects participated each day only so long as they were highly motivated.) Moreover, it should be pointed out that, in terms of a kind of convergent validity, the current findings are wholly consistent with the other studies in this paradigm in which subjects failed to use gaze cues by themselves to locate hidden food (Call *et al.*, in press; Povinelli *et al.*, in press).

Perhaps one reason for chimpanzees' seeming inability to use gaze cues effectively in this and other studies is that gaze by itself is not sufficient to suggest the presence of food – not even in the context of an experiment in which they clearly knew that they were involved in a food-finding game (since they chose a container, and seemingly expected food, on every trial). They apparently need some other behavioral cue from the informant to make gaze direction relevant for finding food. In the current study, the local enhancement cue was intended to resemble a kind of foraging activity in which an individual approaches a food source and remains there looking at it. Subjects apparently found this to be an effective food-relevant cue. This interpretation is supported by the findings of Povinelli and Eddy (1997), who helped chimpanzees to make effective food-relevant choices by having an informant bob her head distinctively (perhaps indicating some form of excitement), and by the findings of Call *et al.* (in press), who were able to indicate the location of food successfully by making the hiding place (a tube) look like one where food was likely to be found – given that chimpanzees naturally and enthusiastically search for food inside holes.

In the current study the chimpanzee informant spontaneously vocalized as she approached the food in the local enhancement condition on three occasions. Interestingly, the subject was successful on all three of these trials. But since subjects were successful in this condition even without a vocalization, this is not a significant finding. Nevertheless, vocalizations are an important aspect of chimpanzee food-related behavior (Goodall, 1986; Hauser, Teixidor, Field & Flaherty, 1993), and so it is possible that vocalizations might represent another food-relevant cue that would make gaze direction more informative for chimpanzees in the object choice paradigm. The second study was designed to explore this possibility.

Study 2

The purpose of this study was to investigate chimpanzees' ability to use a gaze direction cue in combination with vocal information to locate food in an object choice paradigm. In addition to its relevance for the general question of what information chimpanzees need to be successful in this task, the study is also relevant to the question of the 'meaning' of chimpanzee vocalizations. There is currently very little evidence to indicate that chimpanzees or other apes have any vocalizations associated with specific external referents (see Tomasello & Call, 1997, for a review). Therefore, in different

trials we had a human experimenter use one of two different vocalizations. One vocalization was a human version of the chimpanzee 'food-bark', which has a fairly excited emotional tone and is given almost exclusively for food (Goodall, 1986), and the other vocalization was a human nonsense word, articulated without an excited emotional tone (a kind of control procedure). The question was whether chimpanzees would use vocal information at all in this task, and, if so, whether they would use the supposedly food-specific vocalization only.

Method

Subjects

Twelve adult chimpanzees (*Pan troglodytes*) served as subjects, three of whom also had previously participated as subjects in Study 1 (and one of the informants as well). All subjects were housed at the Yerkes Regional Primate Research Center Field Station in small group cages with indoor and outdoor areas. Testing took place in the indoor areas, and animals were fed on their normal schedule throughout testing. Relevant to current concerns, two of the subjects had been raised by humans for much of their infancy and/or childhood: Erika for most of her first 2 to 3 years of life and Peony from about age 1 to 5 (see Premack, 1976).

Materials and design

The set-up was basically the same as the human informant trials in Study 1. The apparatus was basically the same (except smaller), and the human experimenter interacted with subjects from basically the same place in front of their indoor cages (except closer; Figure 1).

There were three different types of experimental trials. All subjects began with 24 gaze trials in which the human experimenter simply turned his head and looked at the baited container, alternating back to the subject several times (Gaze 1 trials). Then there were two 24-trial blocks of two different types of vocalization, with the order of blocks counterbalanced across subjects. In the food-bark trials, the human experimenter turned to look at the baited container, as in the gaze trials, but in addition he produced a chimpanzee 'food-bark' vocalization (five to seven times). This vocalization has a 'throaty', 'breathy' and somewhat excited or insistent quality to it. In the word trials, the experimenter did exactly the same thing except that the vocalization he produced was the nonce word 'Toma' said with a relatively neutral, high-pitched intonation pattern (five to seven times). Each subject then ended with 24

additional gaze trials (Gaze 2). All trials for a given subject were administered within a 1 week period, with daily sessions comprising no more than 24 trials. Food placement was randomized so that each container was baited an equal number of times in each experimental condition for each subject, with the same container never baited three times in a row.

Procedure

All subjects began with four pre-training trials, as in Study 1, in which the experimenter placed food in one of the containers in full view of the subject and then presented the apparatus for a choice. All subjects chose correctly on virtually all of these pre-training trials.

For all types of experimental trials, the same basic procedure was followed. From the hallway in front of the subject's cage, the experimenter raised a cardboard screen on the subject's side of the apparatus (approximately 3 m × 1 m) so that subjects could no longer see the apparatus or the hiding process (although they could see the experimenter's movements from the waist up). The experimenter then baited one container and sham baited the other. He then removed the occluder, made eye contact with the subject, gave the appropriate cue for approximately 10 s, and pushed the apparatus flush to the cage so that the subject could make its choice.

Scoring

A subject's choice for a given trial was the first container it touched. Responses were totally unambiguous (and subjects searched on every trial), so the single experimenter simply noted after each trial which container the subject had chosen.

Results

Performance for each subject in each experimental condition is presented in Table 2. As in Study 1 the primary data analysis compared the number correct against chance, for each subject for each of the four experimental conditions separately. Results showed that for the Gaze 1 cue only two of 12 subjects were above chance; for the food-bark cue six of 12 subjects were above chance; for the word cue five of 12 subjects were above chance; and for the Gaze 2 cue three of 12 subjects were above chance ($p < 0.05$ in all cases).

To assess the relative effectiveness of the four different types of social cue, a few very simple comparisons were made. First, a *t* test established that the two blocks of gaze cues were statistically identical, and so they were

Table 2 Number correct, out of 24, by each subject in each experimental condition in Study 2

	Gaze 1	Word	Food-bark	Gaze 2
Peony	24*	24*	24*	24*
Erika	14	24*	23*	20*
Phinneas	17*	13	17*	20*
Gwinnie	13	11	19*	13
Jesse	15	15	19*	13
Tai	13	16	17*	15
Sheila	13	17*	15	13
Buffy	16	20*	14	9
Cissie	15	18*	16	15
Atlanta	12	13	12	11
Sonya	12	15	13	15
Barbara	10	8	15	14
Average	14.5	16.2	17.0	15.2

Note: * $p < 0.05$, binomial probability.

pooled to make a single Gaze condition. Then, each of the two different vocal cues was compared with this pooled Gaze condition. The food-bark cue was different from the control, $t(11) = 3.11$, $p < 0.02$, whereas the word cue was not. Complicating matters somewhat, however, the two vocal cues were not statistically different from one another.

Patterns of individual performance varied widely across subjects. Three subjects were never above chance on any cue. One subject, human-raised Peony, was above chance, indeed perfect, on all four cues, and two subjects (one of them human-raised Ericka) were above chance on three cues. The other six subjects showed a very interesting pattern. Each of these individuals was above chance on one of the two vocal cues (three for each type of cue), but at chance on both of the Gaze cues, including the Gaze 2 cue which was always given after both the vocalization trials. In five of these six cases, subjects were above chance with the second vocalization cue given.

Discussion

The vocal cues seemed to help many subjects in this task. No subject was successful on a gaze direction cue but not on a vocalization cue, whereas six subjects were successful on a vocalization cue (which included a gaze direction cue) but not on a gaze cue alone (and two of these subjects had also been unsuccessful on both versions of the gaze/point cue in Study 1). Three subjects were successful to some degree on both types of cue. Ericka and Peony, the two subjects raised in infancy by humans, were above chance on both vocal cues and at least one gaze cue, and Phinneas (no special human contact – although early history unknown) was

successful on both gaze cues and one vocal cue. Three subjects were not able to use any of the cues provided in this task to locate the hidden food.

It is surprising that the two different vocal cues were not more different in directing subjects to the baited container. It is surprising because even though the food-bark cue was produced by a human it was quite close – to the human ear at least – to the chimpanzee version, whereas the word cue (with two consonants) was very much unlike anything a chimpanzee is able to produce. In addition, the food-bark cue also, to the human ear, gave the impression of more excitement than the word cue since it was produced with air expelled plosively from the diaphragm. The current findings – limited though they may be since they involve human vocalizations of only two types – thus provide very little support for the proposition that chimpanzee vocalizations encode referent-specific information (for reviews and discussion of this question see Cheney & Wrangham, 1997; Tomasello & Call, 1997).

The question of what specific characteristics of vocalizations are helpful to chimpanzees in locating hidden food is thus, at this point, an open question in need of further research. However, in line with the hypothesis of Study 1, we may posit at least tentatively that a wide range of vocalizations serve to alert chimpanzees that they are in a food-relevant context, which makes their following of the gaze of others relevant for finding food. It is also possible, of course, that the vocalizations in this experiment served some more generic arousal or attention-grabbing function that made the gaze direction of the human more salient. It is even possible that it is the perceived direction of the vocalization – not the content of the vocalization and not the perceived direction of the accompanying gaze – that is the effective cue.

General discussion

The overall pattern of findings across the two studies is clear. When chimpanzees see a conspecific or a human approach a container, look at it and remain beside it (in the context of a food-finding game) they know that food is there. When chimpanzees see a human (and presumably a conspecific) look at a container and vocalize in its direction in this same context, they again know that food is there. When chimpanzees see a conspecific or a human simply gaze and point at a container in the context of a food-finding game, they mostly do not know that this indicates the location of the food – with the major exception that some individuals who have had much experience with humans from an early age can use

this cue quite skillfully (for similar findings on apes with extensive human contact see Call & Tomasello, 1994; Gomez, 1996; Itakura & Tanaka, 1998). In combination with much other evidence in a variety of social-cognitive domains, the latter finding provides further support for the hypothesis that extensive experience with humans causes chimpanzees and other great apes to develop more human-like social-cognitive skills (Call & Tomasello, 1996).

It is highly unlikely that chimpanzees' difficulties in using the simple gaze direction cue derives from extraneous difficulties with the task itself, since they perform almost perfectly in the warm-up trials in which they observe the food being hidden, and since other studies using slightly different experimental arrangements have found similar results. Consequently, our hypothesis is simply that gaze direction does not naturally suggest to chimpanzees the presence of food. Some other behavioral or contextual cue – over and above the simple fact that they are in the process of seeking food – must also be present. To date, the cues that have been found to be sufficient, in combination with gaze direction, to indicate to chimpanzees the location of hidden food are: (1) a food-relevant hiding place (Call *et al.*, in press); (2) head bobbing directed at the subject (in a slightly different paradigm; Povinelli & Eddy, 1997); (3) foraging-type behaviors directed at the hiding place (Study 1); and (4) vocalizations directed at the hiding place (Study 2). Whether any of these cues would be sufficient in the absence of accompanying gaze direction cues remains to be determined.

An interesting comparison in this regard is two recent studies on the gaze following of domestic dogs in an object choice task very similar to that of the current study. Hare, Call and Tomasello (in press) and Hare and Tomasello (1998) presented 11 different individuals (of different breeds and ages) with a variety of gaze and other social cues indicating where food was hidden. The majority of the subjects (8/11) used gaze direction cues, sometimes accompanied by a pointing gesture, quite successfully (much better than chance, and much better than control conditions in which no social cues were given). And they performed equally well with both a human and a conspecific informant. Given this superior performance relative to chimpanzees, one speculation is as follows. Wolves in general evolved as social carnivores that hunt in groups (with dogs descended directly from wolves; Vila *et al.*, 1997), and in group hunting the monitoring of conspecific gaze and head direction is often necessary for effective coordination. Primates, on the other hand, are for the most part herbivorous, and their group foraging does not require the same kind of coordination of movements as the group hunting of

members of the wolf family (the main exception being the chimpanzees of the Tai Forest; Boesch & Boesch, 1989). The demonstrated ability of primates to follow gaze in neutral (non-food) contexts may thus derive from a need to monitor the social activities, not the feeding activities, of conspecifics. To use gaze as a cue for locating food, primates need other information specifying the presence of food specifically.

Our view is thus that gaze following by itself – whether by dogs, chimpanzees or human infants – is not direct evidence one way or the other for the sophisticated social-cognitive skills sometimes called 'theory of mind' (Butterworth & Jarrett, 1991). Although not many species have been studied in the appropriate ways, it is possible that many mammals use the body, head, travel, and gaze direction of conspecifics as indicators of all sorts of external phenomena located in that same direction. The extent to which these organisms understand that conspecifics have visual and other mental experiences as a result of being oriented in a particular direction is a question requiring other research methodologies.

Acknowledgements

This investigation was supported in part by a grant from the National Science Foundation to Tomasello (IBN-9507418), in part by a grant from the Oita Prefecture (Japan) to Itakura, and in part by NIH grant RR-00165 from the National Center for Research Resources to the Yerkes Regional Primate Research Center. The Yerkes Center is fully accredited by the American Association of Laboratory Animal Care. Thanks to Amy Scott for help with data collection.

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Received: 7 June 1998

Accepted: 21 May 1999