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Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*)

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Abstract Five dyads of chimpanzees were tested in a competitive situation, as a pilot study to examine chimpanzees' understanding of conspecifics' knowledge. A human experimenter baited one of five containers in an outdoor enclosure. Chimpanzee A (witness) could see where the food was hidden, while chimpanzee B (witness-of-witness) could not see the baited place but could observe the chimpanzee A watching the food being hidden. Then the two were released into the enclosure. This procedure was repeated for a certain number of days along with a control condition in which neither could see the baited location. The witnessof-witness developed tactics to forestall the witness in two pairs. The witness misled the witness-of-witness by taking a route to an empty container in several cases. These episodes might represent examples of deception. Tactics and counter-tactics thus developed through the interaction between the witness and the witness-of-witness, illustrating the high social intelligence of chimpanzees. An examination of the changes in tactics suggests a possibility that the witness-of-witness understands the witness's knowledge of the location of hidden food.

Key words Chimpanzee · Deception · Tactics · Knowledge attribution

Introduction

Living in a social world is a complicated task. Based on prolonged and repeated interaction with other members of a group, an individual becomes entangled in diverse and dynamic relationships (Hinde and Stevenson-Hinde 1976). With respect to the increasing complexity of primate societies, Humphrey (1976) proposed the hypothesis that pri-

S. Hirata (☞) · T. Matsuzawa Primate Research Institute, Kyoto University, Inuyama, Aichi, 484-8506, Japan e-mail: hirata@pri.kyoto-u.ac.jp, Tel.: +81-568-630567, Fax: +81-568-630085 mate intellect has evolved through selection for social skills in complex societies. Menzel (1971, 1974, 1975) explored the social aspect of the intelligence in chimpanzees living in a 1-acre (0.4 ha) enclosure of a group of infant and juvenile chimpanzees, focusing on their grouping pattern, leadership, and communication. Matsuzawa (1991) conducted a similar study with a group of four 4-year-old chimpanzees in a large outdoor compound. Pieces of food were hidden by experimenters who could be seen by selected individuals who were then tested for their ability to attract naïve members of the group to the baited location. In the series of experiments by Menzel (1974), informed chimpanzees succeeded in leading others to the reward by drawing attention to themselves through actions such as tapping others on the shoulders or repeatedly glancing at them while heading in the direction of the food. Eventually, chimpanzees naïve to the location of the bait seemed to have learned to recognize individuals most competent at finding food and followed them until rewarded. Twenty years after these experiments, Coussi-Korbel (1994) tested a group of seven mangabeys in an experimental design comparable to that of Menzel (1974). She investigated whether monkeys would be able to use firstly a human experimenter and then a conspecific familiar with a baited location as cues to discover hidden food. Using a young male as the informed individual, paired with a dominant but naïve male, revealed an interesting pattern of behaviors: after losing the reward on several occasions to the dominant monkey, the informed male developed a tactic whereby he misled the dominant to his own advantage. By taking an indirect route to the baited location, the young male demonstrated a response akin to a strategy involving tactical deception.

Menzel (1974) did not explicitly test whether the followers understood that the leader knew the location of the hidden food, but the results prompt a question about the chimpanzees' understanding of other chimpanzees' mental states. Recent laboratory studies dealing with non-human primate/human experimenter pairs have shown that chimpanzees and orangutans appear to fail at tasks requiring the attribution of false belief (Premack 1988; Call and Tomasello 1999) but both species seem to understand intention (Call and Tomasello 1998); chimpanzees can discriminate knowledge and ignorance (Povinelli et al. 1990, but see Povinelli 1994) and show empathy in role reversal (Povinelli et al. 1992), while macaques can do neither (Povinelli et al. 1991, 1992). As Matheson et al. (1998) pointed out, the experimental design of Menzel (1974) could be used, in a naturalistic situation, for the study of understanding of others' knowledge under the topic of "theory of mind" – a cognitive framework allowing the interpretation of others' and one's own behavior as a function of various mental states and events – as presented by Premack and Woodruff (1978).

In the present paper, we report a task referred to as "witness and witness-of-witness" incorporating slight modifications to the pioneering work of Menzel (1974). The present experiment was conducted as a pilot study to reevaluate this procedure for investigating chimpanzees' understanding of others' knowledge and ignorance. Chimpanzee A (witness) could see where the food was hidden, while chimpanzee B (witness-of-witness) could not see the baited place but could observe the witness who sees the baiting. We used only two individuals, while Menzel (1974) tested a group of more than four chimpanzees, all together. An important feature of an experimental setting of this type is that the two individuals are in no way controlled by human experimenters, but behave freely from the onset of interaction. Our interests corresponded to those of Menzel (1974) and Coussi-Korbel (1994): the examination of spontaneous behavior developed by two individuals to obtain one piece of hidden food. The first step of the present paper is then to offer a detailed illustration of the natural flow of tactical interactions shown by pairs of individuals: how do the two chimpanzees develop "tactics" to gain access to a single reward? We believe that, to discuss chimpanzees' understanding of conspecifics' states of knowledge underlying interactions, minute description of spontaneous tactical interactions itself deserves reporting, considering that there are only a few published records of this kind (Byrne and Whiten 1990; de Waal 1982). Our question is whether the witness-of-witness understands that the witness knows the location of a hidden food.

Methods

Subjects

The subjects were five female chimpanzees (*Pan troglodytes*) at the Primate Research Institute of Kyoto University (Pendesa, 20 years; Chloe, 16 years; Pan, 13 years; Popo, 15 years; and Puchi, 31 years). They were assigned to five pairs, two of which completed the test conditions. Before this experiment, they had served in various types of experiments on perception and cognitive capacities (Matsuzawa 1985; Fujita and Matsuzawa 1990; Kojima 1990; Tanaka 1995; Tomonaga 1998; Biro and Matsuzawa 1999). All of the subjects lived together in a community of 11 chimpanzees in a semi-natural environment, and had a rich social life including interactions with conspecifics and humans. The housing facility consisted of one large outdoor compound (about 700 m²),

two smaller outdoor compounds with wire mesh roofs, eight indoor rooms, and seven experimental rooms. The three outdoor compounds were enriched with approximately 400 plants of 60 species, climbing structures, and streams (Ochiai and Matsuzawa 1997). The outdoor compounds and indoor rooms were connected to each other by passageways. The chimpanzees were fed three times a day on a diet of fruits, vegetables, and chow. Water was freely available. They were not food-deprived for testing, and they were cared for according to guidelines produced by the Primate Research Institute of Kyoto University.

Apparatus

Five containers (C1–C5) in which a banana could be hidden were set up in the large outdoor compound. A container consisted of a wooden stake fixed to the ground, and an opaque plastic cup attached upside down to the stake approximately 80 cm from the ground. The cup was approximately 25 cm in diameter and 30 cm in depth. Metal parts were installed inside the cup to hold the banana. The banana inside the cup become visible only at a distance of 30–50 cm from the open side of the cup.

General procedure

Testing took place in the morning using the outdoor compound and indoor areas before the daily routine of releasing all the chimpanzees into the outdoor compound. The test began by separating a pair of chimpanzees from the others and guiding them into indoor rooms. After the subjects had arrived in the appropriate room(s), an experimenter entered the outdoor compound and hid a banana in one of the five containers. The identity of the baited container varied pseudo-randomly with the constraint that the same container was not to be used on more than three consecutive days. The two chimpanzees were then released into the compound through a door of an indoor room approximately 3 min after baiting, allowing them to go in search of the banana. All behaviors during the experiments were videotaped, using five cameras in different positions. One trial was run per day. In the course of the experiment, we alternated the two experimental conditions depending on the subjects' behavior, or tactics.

Role-divided condition

In this condition, one of the two chimpanzees could see where the experimenter hid the banana, while the other could not see it directly but was allowed a view of the witness observing the outside. Hereafter, the former subject will be referred to as the witness (W), and the latter the witness-of-witness (WW). Before baiting, the witness entered an indoor room (the waiting room) adjacent to the outdoor compound. The witness could see the outdoor compound through an opening of a half-open door. Also prior to baiting, the witness-of-witness was brought to a second room adjacent to the waiting room. The outdoor compound was totally invisible from this room, but the witness-of-witness could see the witness in the waiting room through a half-open door of this second room. While keeping the two individuals in this state, an experimenter (E1) first showed a banana to both of the subjects, and then entered the compound to hide the banana in a container. E1 left the compound after baiting. After the banana had been hidden, the witness-of-witness was allowed to join the witness in the waiting room. The two individuals were kept together in this room until they were released into the outdoor compound. The sliding door separating the waiting room and the outdoor compound was electrically controlled by another experimenter (E2). E2 opened the door approximately 3 min after baiting, allowing the subjects to exit through the door (Fig. 1).



Fig.1 The witness (Chloe) holding the banana in her mouth and remaining by the container after having just found her reward

Control condition

We conducted a control condition in which neither of the subjects could see where the banana was hidden. Before baiting, the two chimpanzees were brought to the waiting room and the door was closed during baiting. E1 first showed a banana to both of the subjects, and then entered to the outdoor compound to hide the banana in a container. E1 left the compound soon after baiting. E2 opened the door approximately 3 min after baiting, allowing the subjects to exit through the door.

Order of testing and data analysis

A total of five pairs were tested in the following order: Pendesa and Chloe; Pan and Popo; Pan and Pendesa; Popo and Chloe; Puchi and Chloe. However, three of these five pairs did not have any kind of interaction at all and avoided each other. Therefore, we stopped the test and did not explore these pairs further. The present report includes only the other two pairs (pair A: Pendesa and Chloe, and pair B: Pan and Pendesa), which showed some kinds of interaction during the course of the experiments. The behavioral data were analysed from when the two individuals were brought to the room until when one of them obtained the banana, by viewing the five videotapes that recorded all behaviors during the test.

The following four behavioral measures were used:

- A. Threat in the room: threatening behavior toward the experimental partner when kept in the waiting room prior to being released
- B. Seek banana: looking inside a container set up in the outdoor compound
- C. Threat: threatening behavior toward the partner when in the outdoor compound
- D. Wait: stopping all forward movement, turning back to the partner, then staying on the spot, or returning to approach the partner

To illustrate the behavioral changes in pair A in more detail, the following additional measures were used:

- A. Frequency of looking: the number of times Pendesa looked at Chloe during the time they spent in the outdoor compound until one of the two subjects obtained the banana.
- B. Direction of movement: in order to show the change in Pendesa's behavior, all the occurrences of Pendesa looking at

Chloe were subcategorized according to three indices, that is, Pendesa's direction of movement before she looked at Chloe, Chloe's direction of movement at the time Pendesa looked at her, and Pendesa's direction of movement after she had looked at Chloe. Their direction of movement, i.e. which of the five containers they appeared to be heading for, was judged by following their paths. If their choice could not be narrowed down to one container, all possible choices were considered. Pendesa's change in direction of movement before and after she looked at Chloe was categorized into the following four patterns:

- B1. Neglect: Pendesa approached a container different from Chloe's choice after having seen Chloe heading for a certain container.
- B2. Adjust direction: Pendesa changed her route and headed for the same target as Chloe after having seen Chloe approach a certain container (e.g., if Pendesa had headed for container 1, 2, or 3 before she looked at Chloe, but Chloe was on route to container 5 at the time, then Pendesa changed her direction and also approached container 5).
- B3. Neutral: Pendesa, by coincidence on route to the same container as Chloe before having seen Chloe's choice, continued on her path without changing direction (e.g., if Pendesa had been heading for container 1, 2, or 3 before she looked at Chloe, and Chloe was on her way to container 2 or 3 at the time, then Pendesa proceeded to Container 3 without perceptible change in direction)
- B4. Pursue: Pendesa followed Chloe at a distance of less than 1 m or ran after Chloe, while changes in patterns of movement before and after looking at Chloe were same as in "Neutral".
- C. Degree of taking the optimal route (DTOR): a direct optimal route from the door to each container was determined with a width of 2.5 m, considering the pathways the chimpanzees took in everyday situations. The ratio of the length of each subject's travel route that fell within the range of the optimal route to the total length of the travel route was calculated as an index to show the degree of taking the optimal route.
- D. Proximity: the distance between the two subjects while in the outdoor compound was measured every one second until one of them obtained the banana. From a set of these distance values, the mean proximity was calculated for each day.
- E. Misleading behavior: the witness took a route to an empty container after having seen the witness-of-witness coming towards, pursuing, or adjusting direction to the witness.

To illustrate the behavioral changes in pair B in more detail, two additional measures were used:

- Pursue: clearly following or running after the partner from behind
- B. Fight: fight with the partner involving body contact

Results

We provide a detailed description of the course of interactions for pairs A and B.

Pair A (Chloe and Pendesa)

Table 1 provides a summary of the progress of the interaction, focusing mainly on the behavior of Pendesa, who was dominant and served as the witness-of-witness at the final stage after role reversals during the course of the experiment. Pendesa (WW) did not seek the banana for the first 3 days, except on the 2nd day when she happened to come across the banana in one of the containers after the **Table 1** Progress of pair A. The 2nd and 3rd rows from top show the experimental condition, i.e., which role each individual took. The 4th row shows the name of individual who first of went out to the compound when the door opened. The 6-17th rows provide information es about Pendesa's behavior. Asterisks in the 6-11th rows indicate that a particular behavior by

was observed inside the waiting room or in the outdoor compound before one of the subjects obtained the hidden banana. *Numbers* in the *12–16th rows* represent the number of times each behavior was counted. The *last two rows* from top provide information about Chloe's behaviors (*Ch* Chloe, *Pe* Pendesa, *DTOR* degree of taking the optimal route)

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| 25 | | | Pe | Pe | | * | * | * | | | 7 | - | 5 | | | 30 | 54 | | |

Table 2 Day 24 of testing pair A. The banana is hidden in container 4 (C4). The witness (W) is Chloe, the witness-of-witness (WW) is Pendesa

| Time (min:s) | Description |
|-----------------|---|
| 0:00 | Door begins to open. |
| 0:06 | WW puts her head out through the door, looks around. |
| 0:13 | WW enters the compound, goes forward. |
| 0:19 | WW goes to the right at the outdoor booth. |
| 0:23 | W enters the compound, goes straight toward C4. |
| 0:31 | WW looks back in the direction of W. |
| 0:32 | WW changes her route and begins to run toward W. |
| 0:33 | W looks to the right and sees WW coming; stops there, at a distance of about 6 m from C4. |
| 0:34 | W turns to the left, goes toward C2. |
| 0:41 | WW catches up with W on a part of the climbing structure about 2 m from C2. |
| 0:42 | WW looks at W and jumps up overbearingly, W goes away diagonally from WW. |
| 0:43 | WW again jumps up overbearingly. |
| 0:46 | WW sits down on a part of the climbing structure about 3 m from C2. |
| 0:47 | W stops about 4 m away from WW. WW looks at W. |
| 0:49 | W begins to approach C4; WW begins to approach C2. |
| 0:53 | WW looks into C2. |
| 0:56 | W finds the banana in C4. |

| Table 3 Day 28 of testing pair |
|--|
| A. The banana is hidden in |
| container 3 (<i>C3</i>). The witness |
| (W) is Chloe, the witness-of- |
| witness (WW) is Pendesa) |

| Time (min:s) | Description |
|-----------------|---|
| 0:00 | Door begins to open. |
| 0:06 | WW puts her head out through the door. |
| 0:13 | WW enters the compound. |
| 0:16 | WW stops about 2 m ahead of the door, stays there. |
| 0:18 | W puts her head out through the door. WW looks back at W. |
| 0:20 | WW swings her hand threateningly towards W. W makes pout face. |
| 0:22 | WW goes forward. |
| 0:23 | W comes out, goes forward. |
| 0:24 | WW turns back at W, stands up bipedally, and swings arms threateningly toward W. |
| 0:26 | WW goes forward along the right side of the outdoor booth. |
| 0:28 | WW turns back and changes her route to match the direction of W's course. |
| 0:29 | WW walks bipedally in the direction of W's course, swaggering. |
| 0:30 | WW faces W. |
| 0:32 | W stands up. WW stretches both arms around W. |
| 0:33 | WW and W embraces (Fig. 2). |
| 0:34 | WW begins to turn forward and takes her arms away from W. |
| 0:35 | WW and W move apart, heads forward; WW goes ahead of W. |
| 0:38 | WW stops, W comes up just behind WW.WW looks back at W, and orients her rear toward W. |
| 0:39 | W embraces WW from the back. |
| 0:40 | W inspects WW's genital area with both hands. |
| 0:51 | WW moves her body slightly forward. W touches WW's waist, pats and strokes WW's back rapidly with one hand and then the other (Fig. 3). |
| 0:56 | W moves forward looking at WW. |
| 0:57 | W looks at WW; they stare at each other. W goes around trees in front of her from the left, WW does the same from the right. |
| 1:02 | WW goes around the trees and appears in front of W, stays there. |
| 1:03 | WW presents her rear to W. W touches, strokes and rubs WW's left instep. |
| 1:12 | W looks at WW and goes toward C2. |
| 1:14 | WW goes after W. |
| 1:17 | WW overtakes W. |
| 1:19 | W turns to C3, at a distance of about 2 m from C2. WW looks into C2. |
| 1:20 | WW turns back and follows W. |
| 1:25 | W looks back at WW, who is coming up just behind W. |
| 1:27 | W and WW arrives almost simultaneously at C3. |
| 1:28 | WW gets the banana. |

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Fig.2 Pendesa (witness-of-witness, *WW*) and Chloe (witness, *W*) embracing each other (see Table 3). The *arrow* indicates the direction of the baited container (*B*)



Fig.3 Chloe (*W*) touching and tapping Pendesa (*WW*) from the back (see Table 3). The *arrow* indicates the direction of the baited container (*B*)

experimenter inadvertently failed to hide the reward completely. After day 4, Pendesa (WW) began to search through the containers by herself, but she did not display any action toward Chloe (W) until day 11. Role reversal was introduced on day 9. From day 11, Pendesa began to threaten Chloe, the threats being followed each time by Pendesa going to seek the banana by herself, during which time she occasionally (days 13, 18 and 19) found the food along the way before Chloe. After the fourth role reversal, Pendesa (WW) began to adjust her direction of movement to that of Chloe (W) from day 20. More precisely, after entering the compound, Pendesa (WW) first attempted to seek the banana by herself, and then, after Chloe (W) had also emerged, Pendesa began to approach Chloe's route from some distance away. At the same time, Pendesa (WW) began to look at Chloe more and more fre-

 Table 4
 Day 32 of testing pair A. The banana is hidden in container 2 (C2). Neither individual sees the baited location

| Time (min:s) | Description |
|-----------------|--|
| 0:00 | Door begins to open. |
| 0:12 | Pendesa puts her head through the door. |
| 0:21 | Pendesa enters the compound, goes forward. |
| 0:24 | Chloe puts her head through the door. |
| 0:31 | Pendesa looks into C1. |
| 0:32 | Pendesa turns away from C1 and advances. |
| 0:33 | Chloe enters the compound. Pendesa glances at Chloe, shakes her left hand slightly toward Chloe, then heads toward C4. |
| 0:34 | Chloe stops about 2 m from the door. |
| 0:43 | Pendesa looks into C4. |
| 0:45 | Pendesa looks back at Chloe, then goes to C2. |
| 0:55 | Chloe goes forward. |
| 0:57 | Pendesa finds the banana in C2. |

quently. These strategies did not allow Pendesa (WW) to obtain the banana, however, because Chloe (W) always arrived at the baited container before Pendesa had chance to catch up with her. From day 24, Pendesa (WW) began to run ahead of Chloe's (W) path (Table 2). Chloe's (W) initial response was to mislead Pendesa (WW) by taking an indirect route. She succeeded in "deceiving" by performing misleading behaviors on days 24, 25, 27, and 30. On days 26, 28, 29, and 31, however, Pendesa (WW) gained access to the reward by keeping close to and frequently adjusting her direction to Chloe (W) (see Table 3, Figs. 2, 3 for the results of day 28). On the last 3 days of testing this pair, we introduced the control condition. Pendesa exhibited no actions toward Chloe on the 1st day of this control condition (see Table 4 for the results of day 32). The total experimental days were divided into four periods according to Pendesa's change in strategy:

- 1. Period 1: Pendesa only threatened Chloe (days 1–19, during which Pendesa served as the witness-of-witness).
- 2. Period 2: Pendesa began to adjust her direction to Chloe (days 20–27).
- 3. Period 3: Pendesa kept close to Chloe throughout (days 28–31).
- 4. Period 4: control condition (days 32–34). The mean proximity (±SD) between Pendesa and Chloe during the four periods was: 7.3 m (±2.1) during period 1; 7.0 m (±2.0) during period 2; 4.0 m (±2.1) during period 3; 8.0 m (±0.6) during period 4 (ANOVA, *df=3*, *F=2.734*, *P=0.065*). The mean proximity tended to be shorter during days 28–31 than during the other three periods (Fisher's LSD, *P*<0.05 for period 3 vs. periods 1, 2, and 4, respectively). However, towards the end of this experiment Chloe gradually lost her motivation to go to seek the banana, because she had repeatedly been threatened and subsequently lost the reward. Chloe chose instead to stay in a neutral area of the compound</p>

| Tab ditio who | Day | Wit | Wit | Wh | Wh | Pan's behaviors | | | | | | |
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| | 17 | Pendesa | P | \mathbf{Pa} | Pe | | * | | | | | |
| forn serv taine | 18 | | | \mathbf{Pa} | \mathbf{Pa} | | * | | | | | |
| natic ed i: ed th | 19 | | | \mathbf{Pa} | \mathbf{Pa} | | * | | | | | |
| nsid nsid | 20 | | an | \mathbf{Pa} | \mathbf{Pa} | | * | | | | | |
| lbou le th idde | 21 | _ | | \mathbf{Pa} | Pe | | * | | * | | | |
| t Pa e w: in bi | 22 | | | \mathbf{Pa} | \mathbf{Pa} | | * | | | | | |
| n's aitin anan | 23 | | | \mathbf{Pa} | \mathbf{Pa} | | * | * | | | | |
| beh ig ro ia (F | 24 | | | \mathbf{Pa} | \mathbf{Pa} | | * | * | | * | | |
| avic om - 'e Pe | 25 | | | \mathbf{Pa} | Pa | * | * | | | | | |
| or ir ende | 26 | | | Pa | Pa | | * | | | | | |
| A <i>ste</i> 1 the 2.sa, 1 | 27 | | | Pa | Pa | | * | | | | | |
| s out Pa F | 28 | | | Pa | Pa | | * | * | | * | | |
| s in doo 2an, | 29 | | | Pa | Pa | | * | | * | * | | |
| ficat r coi - Pe | 30 | | | Pa I | Pa I | | * | | | | | |
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| nat a und ssa d | 32 | Jeith | | a F | Pa F | * | * | | | | | |
| a pa bef(lid n | 33 3 | זפו | | ⊃a F | e F | | * | | | * | | |
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| ular one anter | 35 3 | | | Da F | Da F | | * | * | | * | | |
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| he su con | 37 3 | | | a F | a F | * | * | | | | | |
| or w ubje npot | 38 | P | Pen | a F | a F | | * | | | | | |
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during the final stage of the test, without paying any attention to Pendesa. Therefore, we decided to discontinue the tests in this pair, to prevent the possibility of Pendesa growing accustomed to Chloe's "indifferent" behavior. When their behavior in the waiting room before being released was examined, they were found to have no interaction with each other. Chloe always stayed far from the exit door and she did not try to approach it until Pendesa had gone through. Pendesa exited through the door when it opened, without paying any attention to Chloe.

Pair B (Pan and Pendesa)

Behavioral change during the course of the experiment is summarized in Table 5, focusing on the behavior of Pan, who was dominant and served mainly as the witness-ofwitness, in order to observe any development in her tactics for obtaining the reward before the witness. On day 1, Pan (WW) set off to seek a banana by herself and found it before Pendesa (W) had even arrived. From the 2nd day onward, Pan's (WW) tactics changed. On day 2, Pan (WW) intimidated Pendesa (W) and obtained the banana by following Pendesa as she took a direct route to the hidden reward (Table 6, Fig. 4). Pan (WW) continued to intimidate Pendesa (W) from this day onward, but Pendesa (W) succeeded in obtaining the banana on day 3 by making a run for the baited container in an unguarded moment of Pan's (WW) (Table 7). From day 4 to day 7, Pan (WW) consistently waited for Pendesa (W) to emerge from the waiting room. When Pendesa (W) went outside the compound, Pan (WW) chased and intimidated her, then found the hidden banana either on the way as she was chasing Pendesa, or by checking every container after having intimidated Pendesa (days 5, 6, and 7; see Table 8 for the results of day 7). Pan (WW) was also seen, during the first 7 days, threatening Pendesa (W) in the waiting room before being released, although Pendesa stayed far from the exit door in the waiting room and did not act against Pan throughout 40 days of testing. We then introduced the control condition on day 8. Pan's overbearing behavior disappeared completely, and she went to seek the hidden banana without paying any attention to Pendesa (Table 9). For the next 3 days of the control condition, no change was observed in general. When the two roles were restored after this control condition, Pan's (WW) behavior returned to its previous repertoire. The above are the results reflecting behavioral change through the first 14 days. The change in tactics in the remaining days was rather different. Pendesa (W) lost her motivation to seek the banana in much the same way as Chloe in pair A. We decided to continue the experiment with this pair. Pan eventually developed a "quick search" strategy. Pan began to quickly search through every container before Pendesa had arrived, or Pan first intimidated Pendesa, thereby preventing her from approaching a container or from entering the enclosure at all, and then checked all the containers one by one. By doing so, Pan had easy access to the banana.

Table 6 Day 2 of testing pair B. The banana is hidden in container 5 (C5). The witness (W) is Pendesa, the witness-of-witness (WW) is Pan

| Time (min:s) | Description |
|-----------------|--|
| 0:00 | Door begins to open. |
| 0:06 | WW runs out into the compound. |
| 0:08 | WW kicks the wall of the outdoor booth. |
| 0:09 | W puts her head out through the door, looks around. |
| 0:10 | WW looks into C1. |
| 0:11 | WW stands bipedally and wanders in the vicinity of C1. |
| 0:17 | W enters the compound, heads toward C5. WW turns back and begins to follow W (Fig. 4). |
| 0:24 | WW catches up with W about 1 m from C5. |

0:26 WW gets the banana at C5, W is about 1 m to the side of WW.



Fig.4 Pan (*WW*) following Pendesa (*W*) who is heading directly towards the baited container (see Table 6). The *arrow* indicates the direction of the baited container (*B*)

Discussion

In two pairs, the witness-of-witness who was ignorant of the baited location displayed a variety of behaviors toward the knowledgeable witness, which would eventually lead to the witness-of-witness obtaining the reward. We observed tactics and counter-tactics developed through interactions within the pair. The results lead us to recognise a highly developed form of social intelligence in the chimpanzee (Humphrey 1976).

The way in which in pair A Chloe (W) often misled Pendesa (WW) by taking an indirect course may represent episodes of "deception" (Whiten and Byrne 1988). A possible explanation might be that Chloe (W) merely forgot the location of the hidden banana. However, this can be refuted by the fact that in the deceptive episode of day 24 Chloe (W) began by approaching the baited location directly and then suddenly changed her course after seeing Pendesa (WW) moving towards her. In addition, Chloe (W) did not actually go all the way to the empty container, but returned to the bait immediately after Pendesa came close to her and paid attention to the empty container. Results from early stages of the tests also suggest that Chloe (W) remembered the baited location well. Another explanation might be that Chloe (W) was merely avoiding Pendesa (WW) because Pendesa was dominant over Chloe. This account of our observations is also unsupported by other evidence. The observation that Chloe (W) and Pendesa (WW) embraced, that Chloe groomed Pendesa, and that Chloe initiated the exchange of glances with Pendesa before proceeding to an empty container during the course of the deceptive episode of day 28 clearly runs counter to the hypothesis that Chloe was merely trying to avoid Pendesa. Therefore, we conclude that Chloe (W) did

Table 7Day 3 of testing pairB. The banana is hidden incontainer 2 (C2). The witness(W) is Pendesa, the witness-of-witness (WW) is Pan

| Time (min:s) | Description |
|-----------------|---|
| 0:00 | Door begins to open. |
| 0:05 | WW runs out into the compound. |
| 0:07 | WW kicks the outdoor booth, and then returns toward the door. W puts her head out through the door. |
| 0:09 | WW, coming back to the door, raises her body upright and lifts her arms toward W. W returns inside when WW charges at the door. |
| 0:10 | WW stays at the door. |
| 0:15 | WW turns and goes toward C1. W puts her head out through the door, looking at WW moving forward. |
| 0:19 | W enters the compound and runs toward C2. |
| 0:20 | WW nears C1, stretches out her arm to touch C1. |
| 0:21 | WW looks at W, twitches her body in the direction of W, and returns to examine C1. |
| 0:23 | WW turns to go to C5. |
| 0:28 | W gets the banana in C2. |

Table 8Day 7 of testing pairB. The banana is hidden incontainer 5 (*C5*). The witness(W) is Pendesa, the witness-of-witness (*WW*) is Pan

| Time (min:s) | Description |
|-----------------|---|
| 0:00 | Door begins to open. |
| 0:05 | WW enters the compound, goes forward. |
| 0:08 | WW stops about 3 m from the door, turns back to the door. |
| 0:09 | WW, facing the door, holds trees with both hands and swaggers. |
| 0:14 | W puts her head out through the door. |
| 0:15 | WW runs back toward W, raising arms toward W. W returns inside. |
| 0:16 | WW follows into the room. W, inside the room, swings her arms towards WW |
| 0:17 | Both stand upright and swing arms towards each other inside the room. |
| 0:18 | WW drives W into a corner of the room. |
| 0:19 | W screams. |
| 0:20 | WW presents genital area to W. W assumes the position of mounting embrace with WW. |
| 0:23 | WW moves away from W and goes to the door. |
| 0:25 | WW enters the compound, stays near the door. |
| 0:27 | WW stands upright, swaggers bipedally near the door. |
| 0:37 | WW swaggers quadrupedally near the door. |
| 0:45 | WW dashes toward C5. |
| 0:46 | WW stops halfway, about 5 m from the door, and returns to the door. |
| 0:49 | W puts her head out through the door and takes a look at WW, then pulls in her head. |
| 0:51 | W puts her head out through the door and looks at WW. |
| 0:52 | WW stands upright, holds trees, and swaggers at a distance of about 3 m from the door. |
| 0:53 | W returns inside. |
| 0:58 | WW goes to C1, reaches into C1 with her left hand and fumbles inside C1. |
| 1:00 | WW looks into C1. |
| 1:02 | WW stays to the side of C1, at a distance of about 3 m from the door. |
| 1:10 | W puts her head out through the door, looks at WW. WW turns to W, stands upright, and holds trees to swagger. |
| 1:14 | W pulls in her head. |
| 1:16 | WW sits down, staying at the same spot. |
| 1:18 | W puts her head out through the door, looks at WW. |
| 1:19 | WW takes a broken branch and strokes the ground with the branch. W returns inside. |
| 1:23 | WW stops stroking the ground. |
| 1:25 | WW approaches to the door. |
| 1:32 | WW stops about 1.5 m to the side of the door, stays there. |
| 1:43 | WW walks two steps further and stands up. |
| 1:47 | W puts her head out through the door, looks at WW. |
| 1:49 | WW swaggers bipedally, W returns inside. |
| 1:52 | W puts her head out through the door, looks at WW. |
| 1:54 | W runs out into the compound toward the left of the door. WW immediately chases W |
| 1:56 | The two get into a scuffle, both are screaming about 10 m from the door in the left of the compound. |
| 1:59 | WW breaks away from W, W pursues WW, both are screaming. |
| 2:07 | WW starts to make a counterattack on W. |
| 2:10 | The two get into a scuffle, both are screaming about 12 m away from the door in the left of the compound. |
| 2:14 | WW runs away from W to the center of the compound. |
| 2:15 | The two get into a scuffle, both are screaming about 7 m away from the door in the center of the compound. W breaks away from WW. WW pursues W, both screaming. |
| 2:16 | WW raises both arms toward W, facing W bipedally. |
| 2:18 | W begins to run toward the right of the compound. WW chases W. |
| 2:22 | W runs away, passes by C5. |

- 2:23 WW nears C5, goes to look into C5.
- 2:24 WW finds the banana in C5. W is still running away.

indeed deceive Pendesa (WW) by making use of the fact that Pendesa had developed the tactic of following Chloe.

Menzel (1974) described similar deceptive episodes. A female juvenile chimpanzee who knew the baited location began to stop uncovering the food when another dominant individual was present, after having the experience that the dominant individual raced over, kicked or bit her, and took all the food. On a few trials she actually misled the group and then rapidly went to the baited location while the dominant individual was away. Together with

 Table 9
 Day 8 of testing pair B. The banana is hidden in container 2 (C2). Neither chimpanzee sees the baited location

| Time (min:s) | Description |
|-----------------|---|
| 0:00 | Door begins to open. |
| 0:05 | Pan enters the compound, runs toward C2. |
| 0:13 | Pan finds the banana in C2. |
| 0:19 | Pendesa puts her head out through the door. |
| 0:22 | Pendesa enters the compound, goes forward |

other observations (for collation of deceptive episodes see Byrne and Whiten 1990), this leads us to conclude that chimpanzees are apparently capable of deceiving other conspecifics by withholding information and misleading.

Another purpose of the present study was to reevaluate this experimental method as assessing the understanding of another conspecific's knowledge. In pair A, Pendesa (WW), when ignorant of the location of the reward, began to take action to obtain it by utilizing the behavior of knowledgeable Chloe (W). The introduction of role reversal could have been an important factor here, because it allowed Pendesa to experience the role of the witness first hand, thus possibly facilitating her understanding of the partner's role. Then, the results of the first day of the control condition in both pairs A and B showed that the behavior of the witness-of-witness was greatly different from the previous pattern. The behavioral change between the role-divided condition and control condition in the two pairs lead us to favor the hypothesis that chimpanzees know of other chimpanzees' possession of knowledge or ignorance. However, we analyzed the interactive behaviors in the two dyads with different set of behavioral categories and used different experimental schedules, due to the great diversity of nature and development of interaction in these pairs. There is a room for further investigation with a more systematic approach and comparative quantitative analysis.

In the study of Menzel (1974), infants and juvenile chimpanzees rarely traveled alone and they needed companions to go somewhere in the enclosure. Thus, the leader chimpanzee who was informed of the baited location should attract other members to go to the hidden food. The fact that the other members followed the leader was generally caused by the leader's invitational behavior. Therefore, the question of whether follower chimpanzees followed the leader with an understanding of the leader's knowledge cannot be solved in this case (Heyes 1998). On the contrary, in the present study conducted with adult chimpanzees, the chimpanzee who was naïve to the baited location spontaneously developed tactics, such as following the knowledgeable partner, to steal the food item. Provided that this kind of tactics are developed by the chimpanzees, we can then go into the question of whether the ignorant individual understands that his/her experimental partner knows the baited location, by comparing the ignorant individual's behavioral pattern between the conditions in which the experimental partner knows or does not know the location of the hidden food.

Recently, Hare et al. (2000) examined whether chimpanzees could understand what other chimpanzees do and do not see, following the research of Povinelli and Eddy (1996) on chimpanzees' understanding of human experimenters' seeing and not seeing. Tomasello et al. (1998) showed that chimpanzees and other non-human primates follow the visual gaze direction of conspecifics, and in addition that the great apes follow and utilize the gaze direction of a human experimenter (Itakura 1996; Call et al. 2000). As Hare et al. (2000) argue, it is important to design a natural social situation to assess what animals know about psychological processes of conspecifics. We believe that our experimental design for examining the animal's understanding of a conspecific's mental state will, when applied to other species as well as re-tested with chimpanzees, contribute to the comparative discussion.

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