Thesis

Behavior and Cognition of Chimpanzees *(Pan troglodytes)* in Social Situations

Satoshi Hirata

Contents

Page

Chapter 1: General Introduction

1-1 General introduction 3-10

1-2 References 11-14

Chapter 2: Tactics to Obtain a Hidden Food Item in Chimpanzee Pairs (Pan troglodytes)

2-1 Introduction 15-17

2-2 Methods 17-22

2-3 Results 22-25

2-4 Discussion 25-28

2-5 References 29-31

2-6 Acknowledgements 32

2-7 Tables 33-42

2-8 Figure Captions 43

2-9 Figures 44-49

Chapter 3: Naive Chimpanzees' (Pan troglodytes) Observation of Experienced Conspecifics in a Tool-Using Task

3-1 Introduction 50-51

3-2 Methods 52-56

3-3 Results 56-60

3-4 Discussion 60-62

3-5 References 63-66

3-6 Acknowledgements 67

3-7 Tables 68

3-8 Figure Captions 69

3-9 Figures 70-73

Chapter 4: General Discussion

4-1 General introduction 74-79

4-2 References 80-82

4-3 Acknowledgements 83

4-4 Table 84

Chapter 1

General Introduction

Comparison of humans with living non-human animal species is a valuable way to explore the evolution of human behavior and cognition, as minds and thoughts are not preserved in the fossil record. In particular, the study of chimpanzees (Pan troglodytes), the closest living relatives of humans, plays an important role in this context. These comparative studies can be roughly divided into two types: experimental study in the laboratory and natural observation in the wild. Köhler and Yerkes began conducting experimental laboratory studies in the 1920s. Köhler (1925) designed various problem-solving situations, and provided detailed descriptions of chimpanzee behaviors in such situations. Famous examples include tool-use experiments, in which chimpanzees used a stick to gather out-of-reach bananas, or climbed up onto a box to get food hanging from the ceiling. Köhler compared the results of chimpanzees with those of humans, dogs, and chickens, to consider the behavior and cognition of humans and chimpanzees from an evolutionary perspective. On the other hand, natural observation of wild chimpanzees in Africa emerged in the 1960s. Its first remarkable achievement was the discovery of tool use by wild chimpanzees. Until this discovery, tool use had been considered unique to humans, but, contrary to this belief, Goodall (1968) observed that chimpanzees in Gombe, Tanzania, used twigs to fish for termites in their mounds. Thus, the ability to use tools observed by Köhler in his laboratory was documented in the wild.

Both experimental studies in the laboratory and natural observations in the wild have advanced since these pioneering works, providing many fruitful results. For example, experimental studies have revealed chimpanzees' ability to use symbols, understanding of numbers, audio and visual processing, self-recognition, and so forth (e.g., Matsuzawa, 1985;

Kojima, 1990; Tanaka, 1995; Tomonaga, 1998; Biro & Matsuzawa, 1999; Kawai & Matsuzawa, 1999; Inoue-Nakamura, 1997). Natural observations in the wild have described in chimpanzees grouping patterns, demographic features, relationships between food resources and activities, reproductive strategies in males and females, and the like (e.g., Goodall, 1986; Sugiyama, 1999; Yamakoshi, 1998). In other words, many experimental laboratory studies have addressed research topics that differ from those of natural observations, and vice versa.

Recently, however, areas of research have been developed that involve both natural observation and experimental study, each with its own research methods. Two of several emerging fields are the most salient. The first can be summarized as social transmission, culture, and social learning; the second as mind reading (understanding the intent of current behavior or predicting future behavior), theory of mind, and complex social interaction. The following is a review of the research within these two areas that employs natural observation and experimental study techniques.

Since Goodall's (1968) discovery, many types of tool use have been observed in Africa. These include "ant dipping", in which chimpanzees use a twig to retrieve ants from an anthill (McGrew, 1974); "nut cracking", in which a hard nut is cracked with a wooden or stone hammer and anvil (Sugiyama & Koman, 1979); and use of a "leaf-sponge", when chimpanzees dip leaves in water and drink from them (Goodall, 1968). Tools are primarily used for obtaining food, but tools such as a "leaf-cushion" may be used for non-subsistence purposes (Hirata et al., 1998). The chimpanzee possesses the ability to use tools in a broad range of situations. Taken together, the reports to date from research sites throughout Africa document more than 30 types of tool in use (McGrew, 1992).

Interestingly, the repertoire of tool use differs between groups of chimpanzees (Whiten et al., 1999). For example, chimpanzees in Gombe, Tanzania, engage in termite

fishing, but the chimpanzees in Tai, Cote d'Ivoire, do not; chimpanzees in Bossou, Guinea, engage in nut cracking of oil-palm nuts, but those in Gombe do not; Gombe chimpanzees eat the nuts' sarcocarp, while those in Mahale, Tanzania, do not. Local differences have been observed not only in tool use, but also in other kinds of behavior. Chimpanzees in Mahale have a special manner of grooming called "hand clasp grooming". Two chimpanzees sit on the ground facing each other, each raising one hand over the head; then they clasp the partner's hand in the air, and groom the side of each other's body. Researchers have never observed chimpanzees in Gombe or Bossou perform this type of grooming. Local differences have also been documented in these populations' hunting behavior, in terms of prey species, use of cooperative hunting, and tool use during hunting (Boesch & Boesch 1989; Uehara, 1999; Hirata et al., in press). These differences are not due to differential genetic inheritance.

Behaviors such as termite fishing, nut cracking, and hand clasp grooming were invented by an individual in a group, and then transmitted to subsequent generations. Given that members of a group know how to crack nuts, newborns in the same group will learn to do so from their mothers or other group members; newborns will not learn to crack nuts if their mothers and other members do not perform nut cracking. Local behavioral differences are caused by transmission of behaviors, not through genetic inheritance, but via some social learning process. Such a phenomenon can be labeled "culture", as first discussed in relation to the observation of potato washing behavior by Japanese monkeys (Kawai, 1965; Hirata, Watanabe, & Kawai., in press).

Social learning and transmission of behavior have also been examined using experimental procedures. Nagell et al. (1993) tested the ability of two groups of chimpanzees to obtain out-of-reach food using a rake-like tool. A human demonstrator showed one group of subjects one way to use the tool, and the other group observed a different method. The

authors concluded that the chimpanzees engaged in emulation learning, in which they paid attention to the general functional relationship between the tool and the food, and to the results obtained by the demonstrator, but subjects did not focus on the actual method employed by the demonstrator. Another effort to investigate social learning in chimpanzees was made by Whiten et al. (1996). They presented chimpanzees an artificial fruit that could be opened by manipulating one of two principal components, each of which could be removed in two alternative ways. Each subject observed only one of the two ways, demonstrated by a human experimenter. Some evidence suggested that chimpanzees were more likely to manipulate a component as demonstrated by experimenters, supporting the existence of imitation. Myowa-Yamakoshi and Matsuzawa (1998) further investigated what kinds of factors determine how hard it is for chimpanzees to imitate actions. Adult chimpanzees were instructed to perform 48 arbitrary actions demonstrated by a human experimenter. Overall, chimpanzees were able to imitate 5.4% of the demonstrated actions in their very first trial, immediately after having observed the human. The authors concluded that actions in which an object is directed toward an external location were easier to perform than those that involved manipulating a single object alone.

Another interesting finding from observations in the field is that social interaction among members of a chimpanzee group can be complex. Both males and females engage in a variety of interactions, such as reconciliation, consolation, and deception (de Waal & Roosmalen, 1979; de Waal, 1982; Byrne & Whiten, 1990; Nishida & Hosaka, 1996). In particular, males form coalition and alliance networks as part of a dominance hierarchy. The struggle for dominance leads to coalition and alliance formation between males, such that competition does not consist of one-to-one fights. Situations have been described, in both captive and wild populations, in which the balance of power among top-ranking male chimpanzees is held by a third individual acting as 'kingmaker' (de Waal, 1982; Nishida,

1983). De Waal (1982) described these coalitions and alliances, along with the allegiance fickleness of males, as "chimpanzee politics". These observations suggest that chimpanzees are capable of predicting each other's future behavior, or even that they are capable of interpreting intent underlying the behavior (Whiten & Byrne, 1998). Deception – to cause an organism to regard a thing or state as being different from the truth – is another conspicuous illustration of the social maneuvering characteristic of non-human primate behavior. Byrne & Whiten (1990) collated evidence for deception in primates observed in captive and wild situations. The authors noted that a significant subset of deceptive episodes included the kinds of behavior that can be expected if elementary forms of mind reading are at work.

The first experimental study to test chimpanzees' ability to read minds was conducted in the 1970s by Premack & Woodruff (1978), with a chimpanzee named Sarah. They coined the term "theory of mind" – a psychological framework for interpreting the behavior of the self and others in terms of various mental states and events, such as wanting, thinking, knowing, and believing – which has been studied using large numbers of human children (Wellman, 1990). Premack & Woodruff (1978) concluded that Sarah's performance in a series of experiments with a human actor constituted evidence that she assigned intention to the human. After a 10-year fallow period, several studies of primates' ability to understand intent have been carried out; results vary according to the kind of ability tested. Povinelli and colleagues conducted a series of experiments using chimpanzee-human pairs. One experiment, using two groups of pairs, concerned role reversal (Povinelli et al., 1992). The chimpanzees of one group knew which of several food containers was baited, and were trained to point to the baited container so that their paired, ignorant human experimenters would pull a lever that allowed access to the food container. Chimpanzees of the other group, who did not know which container was baited, had to pull the lever to which knowledgeable human experimenters pointed. Each group of chimpanzees was then put into the reverse role

with its human partner. As the chimpanzees showed immediate comprehension of the new role, the authors concluded that chimpanzees have the capacity for cognitive empathy. Another test of chimpanzees' ability to discriminate knowledge and ignorance of others used the same apparatus, but a slightly different procedure (Povinelli et al., 1990). The chimpanzees now had to choose one of two human experimenters. One knowledgeable experimenter knew which container was baited because he observed the baiting, and the chimpanzees watched the human experimenter observing the baiting. The other experimenter was ignorant; he left the room before, and came back after, the food had been hidden. Thus, the knowledgeable experimenter gave correct information about the baited location, and the ignorant experimenter gave incorrect information. The results of this experiment indicated that, to some degree, chimpanzees could apprehend ignorance versus knowledge in a human partner (but see Povinelli, 1994). Itakura (1996) studied the ability of 11 primate species (prosimians, monkeys, and apes) to follow a human experimenter's gaze. Only orangutans and chimpanzees reliably oriented to the direction of the gaze, suggesting that these primates can understand the attention structure of others. Experimental studies also have focused on non-human primates' ability to anticipate false belief in others (Premack, 1988; Call & Tomasello, 1999), and to comprehend seeing versus not seeing (Povinelli and Eddy, 1996).

Humphrey (1976) proposed that intellect has evolved in human and non-human primates to handle the unusual levels of complexity that characterize primate societies. This aspect of intelligence is called "social intelligence". Köhler (1925) was already aware of the existence of social intelligence from observations and experiments with captive chimpanzees. He commented, "It is hardly an exaggeration to say that a chimpanzee kept in solitude is not a real chimpanzee at all. Certain special characteristic qualities of this species of animal appear only when they are in a group, simply because the behavior of their comrades constitutes the only adequate incentive for individuals to use a great variety of

essential forms of behavior. Furthermore, the observation of many peculiarities of the chimpanzee will only be clearly intelligible when the behavior and counter-behavior of the individuals in the group are considered as a whole".

In reference to the recent studies in the wild and laboratory reviewed above, it can be said that researchers have begun to investigate social aspects of behavior and cognition via experimental manipulation in the laboratory, in order to sort out the phenomena observed in the wild. Experimental studies on social learning should complement observation of cultural phenomena in the wild, just as experimental studies concerning "theory of mind" and "mind reading" should complement observation of political or tactical interactions, including deception, both in the wild and in captivity. These two types of complementary experimental studies conduced in recent years have features in common: both concern situations in which a chimpanzee is faced with a human experimenter, and both ask whether a chimpanzee can learn something from a human, or whether a chimpanzee can infer a human's mental state. This type of experimental situation plays an important role in investigating the cognitive mechanisms of chimpanzees, because the activity of human experimenters can be controlled to narrow down alternative explanations.

However, if these experimental studies are indeed a counterpart to observations of natural chimpanzee societies, they beg the question of what happens between conspecifics in a similar experimental situation. Very few studies have examined behavior and cognition in a chimpanzee-chimpanzee situation. The following two chapters illustrate two kinds of experimental studies, both of which concern chimpanzee-chimpanzee interaction. The first (Chapter 2) concerns (1) tactical interaction and deception observed in the wild and (2) theory of mind and mind reading examined in the laboratory. Chapter 2 illustrates tactical interaction between two chimpanzees, both trying to obtain a single hidden piece of food. A human experimenter baited one of five containers in an outdoor enclosure. Chimpanzee A

(the witness) could see where the food was hidden, while chimpanzee B (the witness-of-witness) observed not the baiting, but chimpanzee A witnessing the baiting. Then the two were released into the enclosure. This procedure was repeated over several days, along with a control experiment in which neither A nor B could see the baited location. The purpose of this study was to provide a detailed description of the natural flow of the chimpanzees' tactics and counter-tactics, and to examine their revision of tactics in response to comprehension of the other's knowledge. The second study (Chapter 3) concerns (1) cultural differences observed in the wild and (2) social learning examined in the laboratory. Chapter 3 describes behaviors of chimpanzees naive to a tool-use task, honey fishing, when each naive subject was paired with a skilled chimpanzee. Six chimpanzee pairs were presented with 20 kinds of "tools", 12 of which were usable for honey fishing. The study investigated naive chimpanzees' spontaneous observation of experienced conspecifics, and experienced conspecifics' use of enhanced environmental cues.

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Chapter 2

Tactics to Obtain a Hidden Food Item in Chimpanzee Pairs (Pan troglodytes)

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 & Stevenson-Hinde, 1976). With respect to the increasing complexity of primate societies, Humphrey (1976) proposed the hypothesis that primate 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 one-acre enclosure of a group of infant and juvenile chimpanzees focusing on investigating their grouping pattern, leadership, and communication. Pieces of food were hidden by experimenters in view of selected individuals who were then tested for their ability to attract naïve members of the group to the baited location. Informed chimpanzees succeeded to lead 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's (1974). She investigated whether monkeys would be able to use firstly an human experimenter then a conspecific familiar with a baited location as cues to discover hidden food. Using a young male as the informed individual paired up 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 tested whether the followers understood that the leader knew the location of the hidden food, but the results give rise to a question about the chimpanzees' understanding of other chimpanzees' mental state. 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 & Tomasello, 1999) but both species seem to understand intention (Call & 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; Povinelli et al., 1992). As Matheson et al. (1998) pointed out, Menzel's (1974) experimental design could be used, in an 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— 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 Menzel's (1974) pioneering work. 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 altogether.

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 interest 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 only a few published records of this kind (de Waal, 1982; Byrne and Whiten, 1980). Our question is whether the witness-of-witness understand 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 yrs; Chloe, 16 yrs; Pan, 13 yrs; Popo, 15 yrs; and Puchi, 31 yrs). 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 (Biro and Matsuzawa, 1999; Fujita and Matsuzawa, 1990; Kojima, 1990; Matsuzawa, 1985; Tanaka, 1995; Tomonaga, 1998). All of the subjects lived together in a community of 11 chimpanzees in a semi-natural environment, having a rich social life including interactions with conspecifics and humans. The housing facility consisted of one large outdoor compound (about 700m^2), 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 from 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 cared for according to guidelines produced by Primate Research Institute of Kyoto University.

Apparatus

Five containers (C1 – C5) in which a banana would 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 at the height of approximately 80 cm from the ground. The size of the cup was approximately 25 cm in diameter and 30 cm in depth. Metal parts were installed inside the cup as a supplemental device to hold the banana. The banana inside the cup become visible only from a distance in the range 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 three minutes 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 three minutes after baiting, allowing the subjects to exit through the door (Figure 1).

<<< Figure 1 >>>

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 three minutes 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, 3 of these 5 pairs did not have any kind of interaction at all and avoided each other. Therefore, we stopped the test on the way and did not explore these pairs further. The present report includes only the other 2 pairs (Pair A: Pendesa and Chloe, and Pair B: Pan and Pendesa), which showed some kinds of interaction during the course of experiments. The behavioral data was analysed starting when the two individuals were brought to the room until the time 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 as to which of the five containers they possibly headed 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. (b-1) "Neglect": Pendesa approached a container different from Chloe's choice after having seen Chloe heading for a certain container. (b-2) "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). (b-3) "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). (b-4) "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 chimpanzees' pathways taken 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, three additional measures were used. (a) "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 Pairs A and B.

Description of the course of interactions

Pair A (Chloe & Pendesa). Figure 2 provides a summary of the progress of the interaction, focusing mainly on Pendesa's behavior, 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 three days, except on the second day when she happened on her way to come across the banana in one of the containers after the 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 (Day 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 frequently. 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 1). 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 2, Figures 3 and 4 for the results of Day 28). On the last three days of testing this pair, we introduced the control condition. Pendesa exhibited no actions toward Chloe on the first day of this control condition (see Table 3 for the results of Day 32). The total experimental days were divided into four periods according to Pendesa's change in strategy: Period 1, Pendesa only threatened Chloe (Days 1 to 19, during which Pendesa served as the witness-of-witness); Period 2, Pendesa began to adjust her direction to Chloe (Days 20 to 27); Period 3, Pendesa kept close to Chloe throughout (Days 28 to 31); Period 4, control condition (Days 32 to 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, $\underline{df} = 3$, $\underline{F} = 2.734$, $\underline{p} = 0.065$). The mean proximity tended to be shorter during Days 28-31 than during the other three periods (Fisher's LSD, $\underline{p} < 0.05$ for Period 3 vs. Period 1, 2, and 4, respectively). However, Chloe gradually lost her motivation to go to seek the banana towards the end of this experiment due to repeatedly being threatened and

subsequently losing the reward. Chloe chose instead to stay at a neutral area of the compound 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 examining their behavior in the waiting room before being released, 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.

<<< Figures 2, 3, 4 >>>

<<< Tables 1, 2, 3>>>

Pair B (Pan & Pendesa). Behavioral change during the course of the experiment is summarized in Figure 5, focusing on Pan's behavior, who was dominant and served mainly as the witness-of-witness, in order to see the development in her tactics to obtain 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 second 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 4, Figure 6). Pan (WW) continued to intimidate Pendesa (W) from this day onward, but Pendesa (W) succeeded to get the banana on Day 3 by making a run for the baited container in an unguarded moment of Pan (WW) (Table 5). 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 6 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 7). For the next three 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, as opposed to calling it to a halt as in Pair A. 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.

<<< Figures 5, 6 >>>

<<< Tables 4, 5, 6, 7 >>>

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 fact that in Pair A Chloe (W) often misled Pendesa (WW) by taking an indirect course may represent episodes of "deception". 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 attended 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 rejects the hypothesis that Chloe was merely trying to avoid Pendesa. Therefore, we conclude that Chloe (W) did indeed deceive Pendesa (WW) by making use of the fact that Pendesa had developed the tactic of following Chloe.

Menzel (1974) described deceptive episodes similar to the above-mentioned case. A female juvenile chimpanzee who knew the baited location began to stop uncovering the food when another dominant individual was present, after having experienced that the dominant individual raced over, kicked or bit her, and took the food all. On a few trials she actually misled the group and then rapidly go to the baited location wile the dominant one was away. Together with other observations (for collation of deceptive episodes see Byrne and Whiten 1990), chimpanzees are apparently capable of deceiving other conspecifics by withholding the 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 Pair A and B showed that the behavior of the witness-of-witness was greatly different from their previous patterns. 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 more systematic approach and comparative quantitative analysis.

In Menzel's (1974) study, infants and juvenile chimpanzees rarely traveled alone and they needed companion to go somewhere in the enclosure. Thus, the leader chimpanzee who was informed 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 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 whether the ignorant

individual understand that his/her experimental partner knows the baited location, by comparing the former 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 if chimpanzees could understand what other chimpanzees do and do not see, following Poinelli & Eddy's (1996) research 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, in addition to that the great apes follow the gaze direction of a human experimenter (Itakura, 1996). As Hare et al. (2000) claims, 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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Acknowledgements

We gratefully acknowledge S. Suzuki for his assistance and generous guidance throughout the project. Thanks are also due to D. Biro and J. Call for their helpful comments on a draft of this article, and K. Kumazaki, N. Maeda, and other staff at the Primate Research Institute of Kyoto University for support in conducting the experiment and for taking care of chimpanzees. The experiment reported here adhered to the 1986 version of the "Guide for the care and use of the laboratory primates", Primate Research Institute of Kyoto University. The present research was financed by Grant 07102010 and 12301006 from the Ministry of Education, Science, Sports, and Culture, Japan, and also supported by Research Fellowship 9773 from the Japan Society for the Promotion of Science for Young Scientists.

Table 1.

Day 24 of testing Pair A (The banana is hidden in C4. The witness (W) is Chloe, the witness-of-witness (WW) is Pendesa.)

(min:sec)	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 2.

Day 28 of testing Pair A (The banana is hidden in C3. The witness (W) is Chloe, the witness-of-witness (WW) is Pendesa.)

(min:sec)	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 & W embraces (Fig. 3).
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.

(table continues)

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. 4).
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 & WW arrives almost simultaneously to C3.
1:28	WW gets the banana.

Table 3.

Day 32 of testing Pair A (The banana is hidden in C2. Neither sees the baited location.)

(min:sec)	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.

Table 4.

Day 2 of testing Pair B (The banana is hidden in C5. The witness (W) is Pendesa, the witness-of-witness (WW) is Pan.)

(min:sec)	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. 6).
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.

Table 5.

Day 3 of testing Pair B (The banana is hidden in C2. The witness (W) is Pendesa, the witness-of-witness (WW) is Pan.)

(min:sec)	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 6.

Day 7 of testing Pair B (The banana is hidden in C5. The witness (W) is Pendesa, the witness-of-witness (WW) is Pan.)

(min:sec)	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 throughthe 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.

(table continues)

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

(table continues)

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.

Table 7.

Day 8 of testing Pair B (The banana is hidden in C2. Neither sees the baited location.)

(min:sec)	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.

Figure Captions

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

Figure 2. Progress of Pair A. The 2nd and 3rd rows from top show the experimental condition as to which role did each individual take. The 4th row shows the name of individual who firstly went out to the compound when the door opened. The 6th to 17th rows provide information about Pendesa's behaviors. Black circles in the 6th to 10th rows indicate that a particular behavior was observed inside the waiting room or in the outdoor compound before one of the subjects obtained the hidden banana. Numbers in the 11th to 15th 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.

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

Figure 4. Chloe (W) touching and tapping Pendesa (WW) from the back (see Table 2). The arrow indicates the direction of the baited container (B).

Figure 5. Progress of Pair B. The 2nd and 3rd rows from top show the experimental condition as to which role did each individual take. The 4th row shows the name of individual who firstly went out to the compound when the door opened. The 6th to 11th rows provide information about Pan's behaviors. Black circles indicates that a particular behavior was observed inside the waiting room or in the outdoor compound before one of the subjects obtained the hidden banana. Pe: Pendesa; Pa: Pan; –: Pendesa did not enter the compound.

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

8:46:50AM

Day			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Witness			Chloe								Pendesa			Chloe			Pendesa			Chloe														Neither		
Witness-of-witness			Pendesa								Chloe			Pendesa			Chloe			Pendesa															
Who came out first?			Pe	Pe	Ch	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Ch	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe	Pe
Who got the banana?			Ch	Pe	Ch	Ch	Ch	Ch	Pe	Ch	Pe	Pe	Pe	Ch	Pe	Ch	Pe	Pe	Pe	Pe	Pe	Ch	Ch	Ch	Ch	Ch	Ch	Pe	Ch	Pe	Pe	Ch	Pe	Pe	Pe	Pe
Pendesa's behaviors toward Chloe	Threat in the room																																			
	In the compound	Seek banana				●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			●	●	●	●	●	●	●	●	●	●	●	●
		Threat											●	●		●	●	●			●	●		●	●	●	●		●	●	●	●	●	●			●
		Pursue																				●	●		●	●	●	●		●		●			●	●
		Adjust direction																				●					●	●	●	●	●	●	●			
		Wait																											●	●		●				
		Frequency of looking	1	1	0	1	1	0	3	0	0	1	3	2	2	4	1	1	2	1	1	2	4	1	2	5	4	3	6	7	5	12	7	2	10	7
		Neglect					1		2							2	1		1	1	1		1			2	1		1				2		2	1
		Neutral	1	1		1			1			1	3	2	2	2		1	1				1	1	1		1	1	4	4	4	5	4	2	5	5
		Pursue																				1	2		1	3	1	1		2		3			1	1
		Adjust direction																				1					1	1	1	1	1	4	1			
		DTOR (%)	7	100	21	9	11	8	59	5	100	100	100	4	2	6	24	100	18	24	10	4	23	4	11	19	19	3	33	46	14	46	35	17	2	30
Chloe	DTOR (%)		100	100	100	100	100	100	41	100	5	12	17	100	100	100	63	9	9	24	17	100	100	100	100	58	38	100	73	59	100	72	42	100	6	54
	Misleading behavior																									●	●		●	●		●				

Fig. 2 Hirata

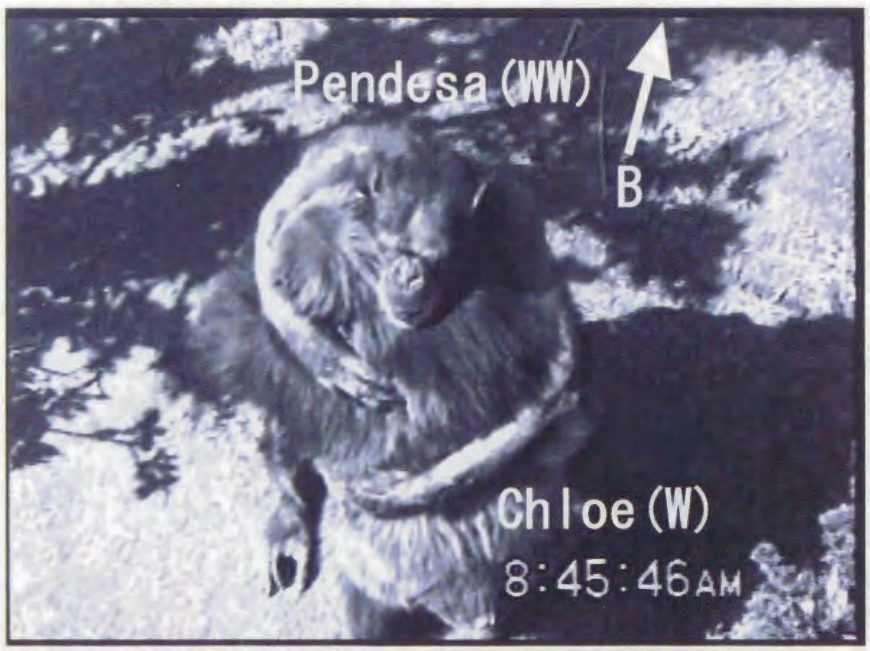

Fig. 3

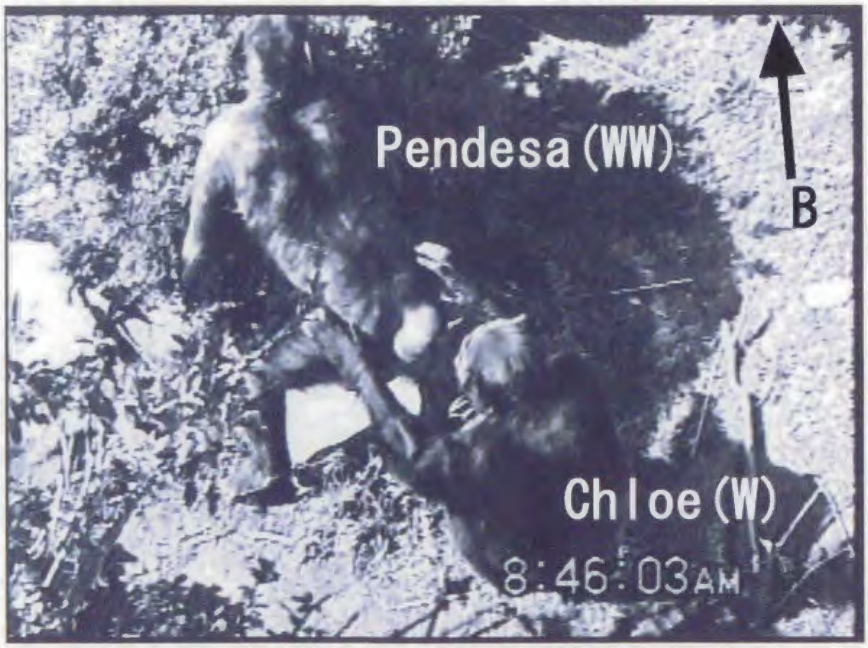

Fig. 4

Day			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Witness			Pendesa							Neither				Pendesa																Neither										Pan		
Witness-of-witness			Pan											Pan																										Pendesa		
Who came out first?			Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa
Who got the banana?			Pa	Pa	Pe	Pe	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pe	Pe	Pa	Pe	Pa	Pa	Pa	Pe	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pa	Pe	Pa	Pa	Pa	Pa	Pa	Pa	Pa
Pan's behaviors toward Pendesa	Threat in the room		●	●	●	●	●	●	●						●												●							●					●			
	In the compound	Seek banana	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
		Threat			●	●	●	●	●					●	●										●	●				●							●					
		Pursue		●		●	●	●	●						●								●								●											
		Wait			●	●	●	●	●			●			●			●								●				●	●				●	●	●					
		Fight				●	●		●																																	

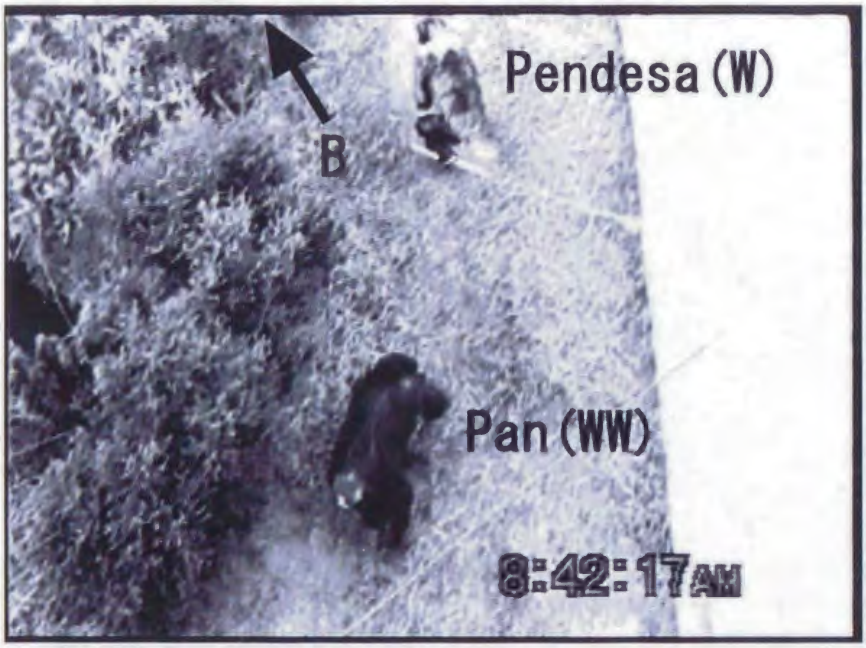

Fig. 6

Chapter 3

Naive Chimpanzees' (Pan troglodytes) Observation of Experienced Conspecifics in a Tool-Using Task

Introduction

Tool use in chimpanzees and other animals has been a major focus of the study of their causal understanding of object relationships and also of social learning. Wild chimpanzees use a variety of tools McGrew, 1992), including those for nonsubsistence purposes (Hirata, Myowa, & Matsuzawa, 1998). Longitudinal observation at several different study sites in Africa has shown the diversity in the wild chimpanzees' repertoire of tool use among different sites (Whiten et al., 1999). Experimental studies have also documented the propagation of tool use and object manipulation among group members of chimpanzees in the wild (Inoue-Nakamura &Matsuzawa, 1997; Matsuzawa, 1994; Matsuzawa & Yamakoshi, 1996) and in captivity (Paquette, 1992; Sumita, Kitahara-Frisch, & Norikoshi, 1985; Tonooka, Tomonaga, & Matsuzawa, 1997). Collectively, these studies suggest that social influences play an important role in the transmission of tool use within each population (e.g., Boesch, 1991; Matsuzawa, 1999). Researchers have attempted to sort out the mechanism of social learning by making a situation in which chimpanzees were exposed to human demonstrators (Nagell, et al., 1993; Whiten, et al., 1996). However, few researchers have examined tool use by using a conspecific as a demonstrator (Paquette, 1992; Sumita et al., 1985). By making a situation in which naive individuals stay with skillful conspecifics, we can simulate the phenomenon that occurs naturally in the wild. The first and most important thing for a naive individual to do in such a situation is to observe skillful conspecifics. Moreover, they ought to observe a model before

their first attempt or after their own failure to learn efficiently how to use a new tool. The observation of a model ought not to occur randomly; rather, it should be contingent on the result of their preceding attempts. There has been no study in which these points were analyzed in detail.

An observation of the innovation and propagation of a tool-using feeding technique in wild vervet monkeys provides another view (Hauser, 1988). Hauser indicates that an animal might acquire the technique from obtaining the end product of an innovator without having observed its technique. He further suggests that learning from the use of abandoned materials can be another way for the social transmission of a new technique, in addition to learning from direct observation of a demonstration.

We designed our experimental study in such a way that we could examine the occurrence and the timing of naive chimpanzees' spontaneous observation of experienced conspecifics, as well as the use of abandoned tools. Adult and adolescent chimpanzees were brought to a "honey-fishing" task in which they had to use tools to obtain honey in a bottle. Chimpanzees could honey fish by inserting a short, slender, flexible tool into a hole of a honey bottle and dipping it into the honey. This technique is similar to that of ant fishing or termite fishing, which wild chimpanzees of some populations engage in (for a description of these activities in Mahale, see Nishida, 1973; for a description of these activities in Gombe, see van Lawic-Goodall, 1968;). We brought a skilled individual and a naive individual together to the honey-fishing situation, and we investigated whether the naive individual would observe the skilled partner . In the present article, we describe the sequence of the chimpanzees' observing their partners, along with the cases of use of left-over tools.

Method

Subjects and Housing Conditions

The subjects were 9 adult and adolescent chimpanzees (Pan troglodytes) at the Primate Research Institute of Kyoto University, Inuyama, Aichi, Japan. Two of them were males (Gon, 32 years; Akira, 21 years), and 7 were females (Puchi, 32 years; Ai, 21 years; Mari, 21 years; Pendesa, 21 years; Chloe, 17 years; Popo, 16 years; Pan, 14 years). Before this experiment, some of them had served in various types of experiments on perception and cognitive capacities (Biro & Matsuzawa, 1999; Fujita & Matsuzawa, 1990; Kawai & Matsuzawa, 2000; Kojima, 1990; Matsuzawa, 1985; Matsuzawa, et al., 1997; Myowa-Yamakoshi & Matsuzawa, 1999; Tanaka, 1995; Tomonaga, 1998). In addition, all of them had served in a tool-using experiment in which they used leaves for drinking juice (Tonooka et al., 1997). All of the chimpanzees lived together in a community of 11 chimpanzees in a seminatural, enriched environment, having a rich social life that included interactions with conspecifics and humans. The housing facility consisted of one large outdoor compound (about 700 m^2), two smaller outdoor compounds with wire mesh roofs, eight indoor rooms, and seven experimental rooms. The three outdoor compounds were enriched with streams and approximately 400 plants of 60 species, climbing structures up to 15 m high (Ochiai & Matsuzawa, 1997). The outdoor compounds and indoor rooms were connected to each other by passageways. The chimpanzees were fed various fruits and vegetables three times a day . Water was freely available, and they were not food deprived for testing. They were cared for according to guidelines produced by the Kyoto University Primate Research Institute.

Materials

Twenty kinds of objects were presented as "tools." The tools varied in material, shape, and size, with a range of 6.5 to 20.0 cm in length. Eight kinds of these objects were "unusable tools" (i.e., a stick, spoon, bolt, pouch, pin, chain, and two types of brushes) that could not be inserted into the honey hole because because of the size of the object. The remaining 12 kinds of objects were "usable tools" (i.e., various types of short and slender objects made of metal, plastic, cotton, and hemp) that could be inserted into the hole. The chimpanzees may have seen or played with similar objects (e.g., strings, wires, spoons, brushes, bolts, or pouches), but they had never seen exactly the same objects before the present experiment. A transparent polyethylene bottle ("honey bottle," 4.0 cm long, 2.5 cm wide, and 6.0 cm high) was used as a container for honey. A hole 5 mm in diameter was made in one side of the honey bottle, approximately 4 cm from the bottom. Honey (about 35 g in volume) was put into the bottle, keeping it under the level of the hole.

Procedure

Single-subject condition Three chimpanzees, Pan, Puchi, and Ai, were tested individually in a familiar playroom (5.0 m long, 7.2 m wide, and 3.0 m high; Figure 1). The walls of the room were partly constructed with transparent acrylic panels. In one of the panels was a hole 5 mm in diameter and 92 cm from the floor. A honey bottle was fixed from outside the room to the acrylic panel in such away that the holes of the bottle and panel fit each other. Two items of each of the 20 kinds of tools were scattered in a completely random manner on the floor within 2 m of the honey bottle. There were also some plants and a fish tank for environmental enrichment of the playroom, and these plants could be used as a tool in addition to the 20 kinds of tools provided. To help the chimpanzees recognize that the bottle contained honey, a human experimenter inserted a tool into the hole before the start of each test.

Chimpanzees thus could get honey merely by pulling out the already inserted tool in the beginning of the test session. A session started as soon as a chimpanzee was brought to the room and lasted for 60 min maximum. The session was ended after 30 min if the chimpanzee had not obtained the honey and had stopped touching the tools. All test sessions were recorded on videotape using two video cameras. One video camera was fixed in front of the honey bottle and filmed the close-up view of the chimpanzees' honey-fishing activity. The other video camera followed all the chimpanzees' movements during the sessions.

Pair condition When the chimpanzees that were tested in the single-subject condition had mastered the tool-using skill, they were paired with the naive individuals. A pair (consisting of an experienced and a naive individual) was brought in the playroom to the honey-fishing situation. When naive chimpanzees had acquired the tool-using skill in this pair condition, some of them were paired with other naive individuals and then served as the experienced chimpanzee in the next turn. A total of six pairs were formed in this manner. Two identical honey-fishing sites were prepared (Figure 1). Each site consisted of a honey hole, a honey bottle, and 2 of each of the 20 kinds of tools randomly scattered on the floor. One of the two sites was exactly the same as that used in the single-subject condition. The other site was positioned at an angle 90° from the first one. The distance between the two holes at these sites was 2.2 m. One session lasted for 60 min maximum. The session was ended when the two honey bottles became almost empty, and none of the chimpanzees had touched the tools for more than 5 min. Five sessions were conducted for each pair. All test sessions were recorded on videotape using four video cameras. Two of the video cameras were fixed in front of the two honey bottles and filmed the close-up view of the chimpanzees' honey-fishing activities. The other two video cameras recorded all the chimpanzees' movements during the session.

<<< Figure 1 >>>

Data Analysis

The chimpanzees' behaviors were analyzed by reviewing the videotapes. First, chimpanzees' honey-fishing attempts were scored. An *attempt* was defined as a sequence of behaviors that began when a chimpanzee inserted a usable tool into the hole or when it touched the acrylic panel within approximately 20 cm of the hole with an unusable or usable tool; the attempt ended when the chimpanzee detached the tool from the acrylic panel. Thus, one attempt involved one tool.

The result of each attempt was divided into two categories: (a) success—the chimpanzees were able to dip honey with the tool, and (b) failure—the chimpanzees were unable to dip honey. The failure was further divided into two categories: *tool-choice error* and *technical error*. Failures with unusable tools were defined as tool-choice errors, whereas failures with usable tools (e.g., when the tool went upward or straight instead of bent towards the honey) were considered technical errors. The success rate was calculated by dividing the number of successes by the total number of attempts. The tool-choice error rate was calculated by dividing the number of tool-choice errors by the total number of failures.

In the pair condition, all occurrences of the chimpanzees' observation of the partner within the range of 1 m were analyzed (Figure 2). There were two directions of observations (naive toward experienced and experienced toward naive). It could be clearly distinguished whether a chimpanzee was observing its partner or not, because chimpanzees approached the partner very closely when observing its attempts in all cases. These observation episodes were coded independently by two individual coders to assess interobserver reliability. Although there were slight disagreements on the starting and ending time in several cases, each observation

episode scored by a coder corresponded one-to-one to the other's score. The behaviors of both chimpanzees before, during, and after the observation were also analyzed from the videotape. The observers' sequence of behaviors were divided into three categories: (a) success—chimpanzees observed their partner after their own successful attempts, (b) failure—chimpanzees observed their partner after their own failures, and (c) immediate—naive chimpanzees observed their partner before having had the first experience of successful or unsuccessful attempts to use tools by themselves.

<<<Figure 2>>>

Results

Process of Acquisition of the Task

Of the 3 chimpanzees who were tested in the single-subject condition, 2 (Pan and Puchi) became skillful in using tools. The success rates of both Pan and Puchi constantly increased as sessions went on. Pan reached over 70% success in the 3rd session, and Puchi obtained the same rate in the 6th session. The other individual, Ai, did not become a proper tool user, and we stopped the test on the 10th session because she made no attempts at all in the 6th, 8th, 9th, and 10th sessions. In the case of chimpanzees tested in the pair condition, 4 of the 6 naive chimpanzees became skillful in using tools. The other 2, Popo and Akira, did not use tools properly. The success rates of these 2 unsuccessful chimpanzees did not reach over 20% throughout the sessions, and they attempted much less frequently after several failures. Figure 3 shows the change in success rates of the 3 chimpanzees tested alone and the 6 naive chimpanzees tested with experienced partners over the first 3 sessions.

The 6 chimpanzees who became able to use tools (i.e., the 2 chimpanzees tested alone and the 4 naive chimpanzees tested in pairs) showed the following in common: (a) many tool-choice errors and the use of a variety of tools in the first session, (b) then a gradual reduction of the tool-choice errors as sessions went on (Figure 4): repeated measures analysis of variance (ANOVA), $F(2, 5) = 14.29$, $p < .01$. There was also a decrease in the number of types of tools used (the mean number of tool types used by these 6 chimpanzees in the first, second, and third sessions was 7.8, 3.5, and 3.7, respectively; *t* tests revealed significant differences between the first and the second and the first andthird sessions, $p < .01$ in both cases).

<<< Figure 3 and 4 >>>

Observation of the Partner

In the pair condition, the participants approached their partners to observe their activity of using tools. There were 40 observation episodes among six pairs in the first three sessions summarized in Table 1. Most of the observations took place in the first session (28 out of 40, or 70%). The number of observations during the first session tended to be larger than that during second and third sessions for each pair: $p < .05$, sign test, one-tailed.

With respect to the behavioral sequences of observation, naive chimpanzees never observed their experienced partners after their own successes, but they did so immediately after their failures, after abandonment, or before their first attempt (see Table 1). On the other hand, all of the six cases of experienced partners' observations took place after their successes. The distribution of these observation episodes was statistically tested by Fisher's exact test for each chimpanzee to see if this inclination had been caused by the fact that the naive chimpanzees had more occasions to observe the partner after their failures because they had a larger number of failures, and by the opposite fact in the case of experienced partners. The results showed that

Pendesa and Mari, both naive chimpanzees, observed their experienced partners significantly more often after their failure attempts than after successful attempts ($p < .001$ both for Pendesa and Mari). The other 4 individuals observed their experienced partner just once. When the data were pooled into naive chimpanzee group and experienced chimpanzee group, a significant inclination to observe after failures was found in the naive chimpanzee group ($p < .001$, Fisher's exact test) but not in the experienced chimpanzee group ($p = .49$, Fisher's exact test).

<<< Table 1 >>>

The following are brief explanations of the events around the naive chimpanzees' first observation of tool use by experienced partners. Of the 2 naive chimpanzees that observed the experienced partner before their own first attempt, 1 used the same tool as the partner after her observation and immediately succeeded with it, while the other failed with a different tool. Of the 3 naive chimpanzees that observed their partner after their own failure attempts, 1 used the same tool as the partner's choice and succeeded, another failed with a different tool, and the other did not attempt to use a tool after observing the partner. The remaining naive chimpanzees did not observe their experienced partners at all.

Two naive chimpanzees observed their partners more than once. However, after their own first success, their choices of tools were not affected by these observations of the partners. They sometimes went to observe the partner after their own failures, but they tended to be persistent in their previous tool choices even after they had observed the partner succeeding with different kinds of tools.

Use of the Partner's Left-Over Tool

Four naive chimpanzees used their partners' left-over tool 10 times (2 to 4 times per individual). Seven out of the 10 cases occurred in the first session. Nine cases occurred after an

experienced individual left the honey-fishing site with a tool inserted in the hole, and then a naive chimpanzee came to take it. The remaining case was "robbing"—an active taking of the partner's tool. A naive chimpanzee approached its experienced partner that was using a tool and took the tool out of the hole as the experienced partner was inserting it. This occurred after the naive chimpanzee's own failure. In another case, a naive chimpanzee succeeded for the first time by using a tool used previously by its partner. Out of a total of 38 attempts in the 10 cases where the naive chimpanzees used a "borrowed" tool, 25 were successes (66 %), and the rest were technical errors. In the same sessions, the success rate of their own tool choices was 36% on average, and they showed an average tool-choice error rate of 28%.

Comparison of Tool-Use Acquisition Between the Two Groups

The time of the first success of chimpanzees tested in the single-subject condition was (a) Pan: 10 min, 15 s in the first session; (b) Puchi: 1 min, 51 s in the second session; and (c) Ai: 12 min, 6 s in the third session. The first successes of all the naive chimpanzees tested with experienced partners occurred in the first session and those latencies were (a) Pendesa: 20 min, 0 s; (b) Chloe: 5 min, 59 s; (c) Popo: 22 min, 45 s; (d) Mari: 1 min, 8 s; (e) Gon: 4 min, 2 s; and (f) Akira: 1 min, 46 s. With respect to the comparison of tool-use acquisition between the single-subject condition and the pair condition, no clear difference was found between the chimpanzees tested alone and the naive chimpanzees tested with experienced partners in terms of the latency to the first success (Mann–Whitney U test, $p = .10$) and the change in success rate over sessions, even if the unsuccessful chimpanzees were excluded (see Figure 3). A two-way ANOVA revealed no significant effect of test condition: $F(1, 8) = 1.34$, $p = .31$, and no significant interaction between test condition and session, $F(2, 8) = 0.60$, $p = .57$).

Discussion

The present study provided a view on how chimpanzees respond to conspecifics in a tool-using situation when a naive chimpanzee was given the opportunity to observe an experienced model. The naive chimpanzees actually went to observe the experienced conspecifics at a very close distance. Most of these observations occurred in the initial stage of the naive chimpanzees' experience with the task. From a longitudinal study of the development of stone use for cracking nuts in wild chimpanzees, Matsuzawa (1999) pointed out the importance of infants' long-term, active observation of the other members of the community and the tolerance shown to the infants' spontaneous attempts, including "robbing." In addition, van Schaik et al. (1999) pointed out the importance of tolerance in facilitating social learning. If an animal cannot approach another because of the risk of attack caused by a dominance relationship, the animal cannot learn well by observation (Coussi-Korbel & Fragaszy, 1995). The chimpanzees in the present study were tolerant enough to allow their partners to come close to observe them, and the naive observers spontaneously approached to do so.

The timing of the naive chimpanzees' observations of their partners made it clear that the naive chimpanzees never went to observe their experienced partners after a successful attempt, with the proviso that most of the data came from 2 chimpanzees. They went to observe their partners after their failure or before their first attempt. The observation of the partner occurred in an efficient pattern to improve their own attempts to use the tool. This is the first step for chimpanzees to learn socially about actions. That they can do so has been confirmed by experimental studies in which a chimpanzee observed a human model (Nagell et al., 1993; Whiten et al., 1996). The present study of chimpanzees in captivity clearly demonstrated that the they show the tendency to achieve this first step by themselves. On the other hand, the

experienced partners also went to observe the naive chimpanzees' ineffective manipulation of tools. Close observation by these individuals may show their simple interest in the others' activities or altruistic concern for the unsuccessful partner. On the other hand, perhaps it can be more generally discussed in terms of stimulus enhancement, but further analysis on the nature of these cases could not be conducted because of the low frequency of these episodes.

No clear difference was found between the single-subject group and the pair group in the number of sessions to needed to acquire the skill. This might indicate that the honey-fishing task could be learned just as efficiently through individual problem solving, as suggested by researchers who conducted a study on sponge-making by a captive chimpanzee (Kitahara-Frisch & Norikoshi, 1982). However, given that an individual in the single-subject group mastered this task quite quickly, it may be that the task was too simple for social learning to give a measurable advantage in acquiring the skill. Taking an example from wild chimpanzees, it takes 3.5 to 5.0 years for infants to master nut-cracking behavior, which is much longer than it takes for other kinds of tool use, such as ant-dipping or use of leaves for drinking water. These skills are acquired by 2-year-olds of the same population (Matsuzawa, 1999). Matsuzawa (1999) explained this difference according to the number of relations involved in these tool-use skills. Ant dipping or honey fishing involves only one relation (relating a twig to ants or relating a wire to honey), whereas nut cracking involves two relations (relating a nut to an anvil stone and then relating a hammer stone to this set). In a relatively difficult task that involves two relations, such as nut cracking, the infant's spontaneous observation of the its mother or another group member in an appropriate behavioral pattern may play a more important role in acquisition of the skill. Future studies in which researchers use more difficult tasks may demonstrate the effect of the conspecific model in social learning.

We observed a physical condition that possibly facilitates the transmission of tool use. The unskillful naive chimpanzees used the tools left in the hole by their experienced partners. There was also a single case in which a naive chimpanzee robbed or actively took the partner's tool. These phenomena suggest other possible ways for naive animals to benefit from the activities of experienced partners as they acquire a new skill in tool use. In the present study, the activity of skilled animals set an appropriate environmental condition where tools were left in close distance from the food, which provided another means for naive animals to learn the relationship between the tool and the food. This finding is consistent with the result of another experimental study in a captive group in which several chimpanzees first acquired the skill of drinking juice by using leaf tools that were abandoned by a skilled individual Tonooka et al., 1997).

The present study is the first to carefully examine tool-use acquisition using conspecifics as sources of information. The results clearly demonstrated two important factors for the transmission of tool use: close observation of a skilled individual in action and enhanced environmental cues provided by a skilled individual. The transmission of tool use in the wild that results in the great diversity in tool repertoire might have been accomplished through a mixture of individual learning aided by such a favorable physical condition and active observing of conspecifics in an appropriate timing for observational learning.

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Acknowledgements

The present research was financed by Grant 07102010 from the Ministry of Education, Science, Sports, and Culture, Japan. We gratefully acknowledge T. Matsuzawa for his idea of "honey fishing" and his generous guidance throughout the project. Thanks are also due to D. Fragaszy and M. Celli for their helpful comments on an early draft of this article, and to K. Kumazaki, N. Maeda, and the other staff members at the Primate Research Institute of Kyoto University for support in conducting the experiment and for taking care of the chimpanzees.

Table 1.

Observation of the partner

Direction and Pair (E & N)	Session 1st	Session 2nd	Session 3rd	Total	Event before Observation: Success	Event before Observation: Failure	Event before Observation: Immediate
N to E							
Pan & Pendesa	4	3	0	7	0	6	1
Puchi & Chloe	1	0	0	1	0	1	0
Pan & Popo	0	0	0	0	0	0	0
Chloe & Mari	16	4	4	24	0	24	0
Puchi & Gon	1	0	0	1	0	0	1
Pendesa & Akira	1	0	0	1	0	1	0
Subtotal	23	7	4	34	0	32	2
E to N							
Pan & Pendesa	1	0	0	1	1	0	-
Puchi & Chloe	3	1	0	4	4	0	-
Pan & Popo	1	0	0	1	1	0	-
Chloe & Mari	0	0	0	0	0	0	-
Puchi & Gon	0	0	0	0	0	0	-
Pendesa & Akira	0	0	0	0	0	0	-
Subtotal	5	1	0	6	6	0	-
Total	28	8	4	40	6	32	2

Note. N to E; Naive observed Experienced, E to N; Experienced observed Naive.

Figure captions

Figure 1. Experimental arrangements of the honey bottle, the hole, and tools in the playroom (top view). The single-subject condition was conducted using A. The pair condition was conducted using A and B.

Figure 2. A naive chimpanzee (right) observing an experienced one (left).

Figure 3. Success rate of the 3 chimpanzees tested in the single-subject condition and the 6 naive chimpanzees paired with the experienced partners in the pair condition over the first three sessions. A pound sign (#) represents a successful individual.

Figure 4. Mean tool-choice error rate (+*SD*) of the 6 successful chimpanzees over the first three sessions. Tool-choice error rate was calculated as the number of tool-choice errors divided by total number of failures (i.e., tool-choice errors plus technical errors).

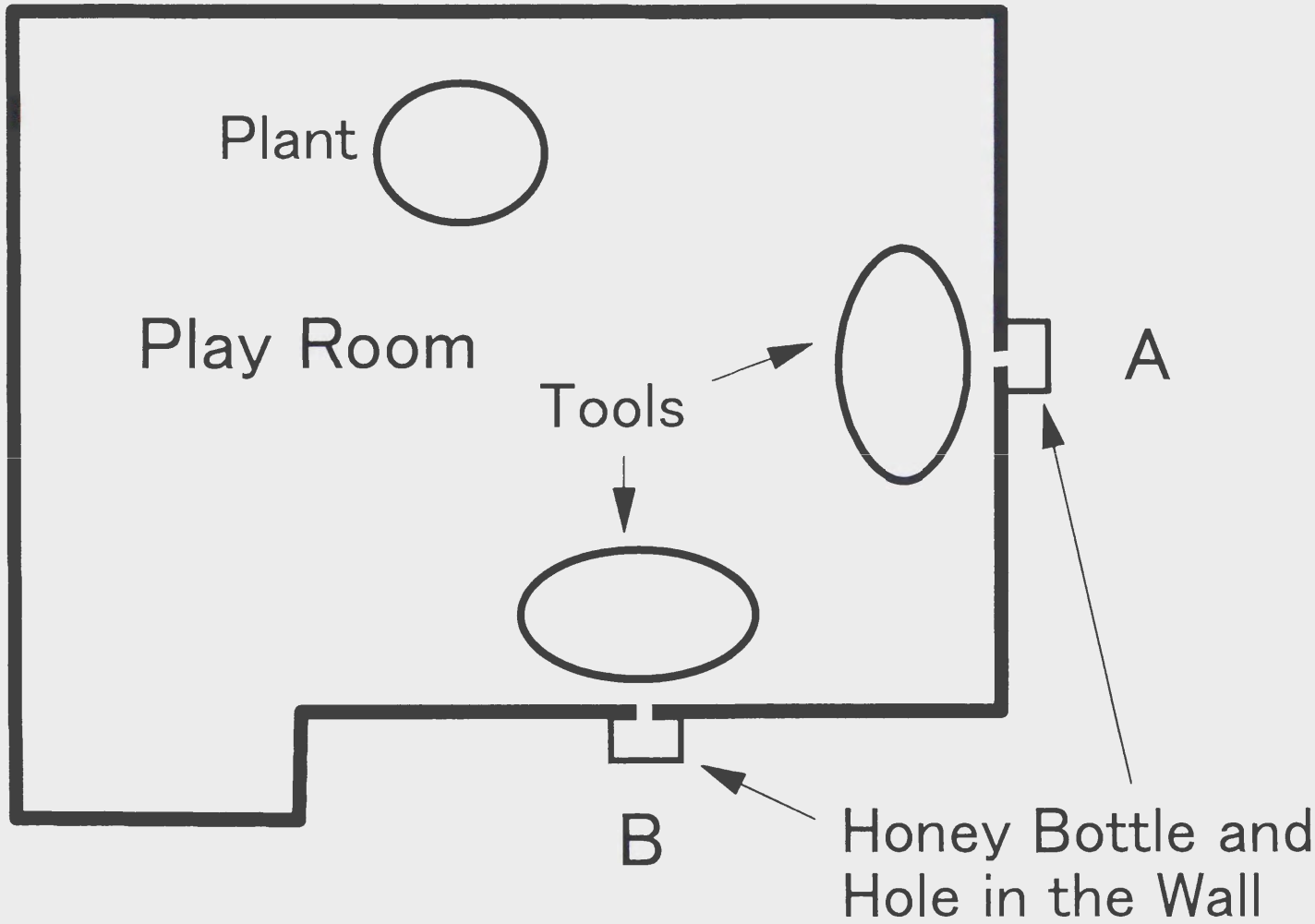


fig. 1

Fig. 2

Fugure 3

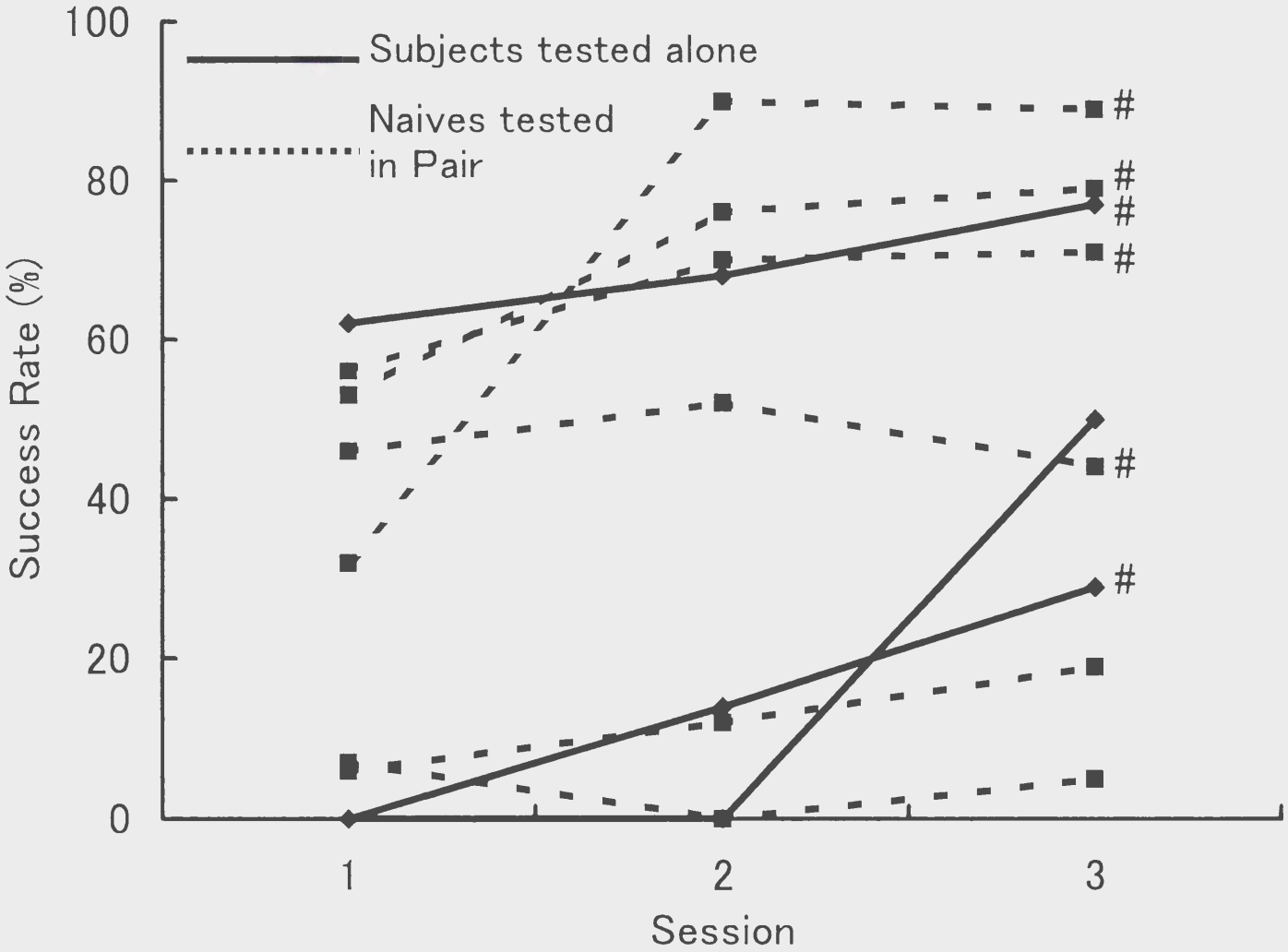
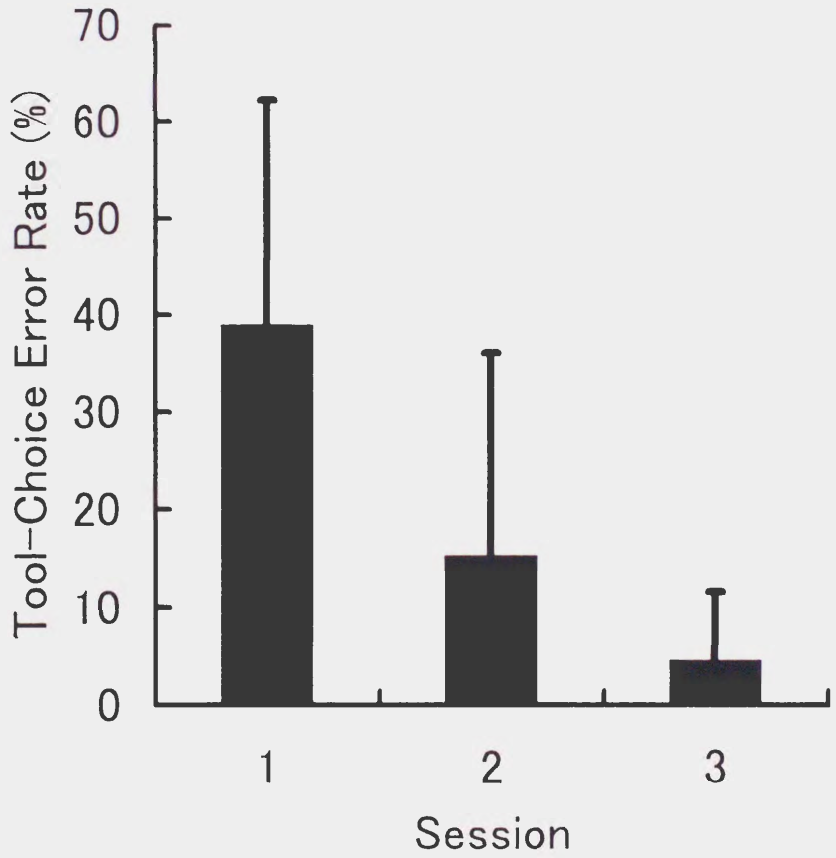

Subjects tested alone
Naives tested in Pair
Success Rate (%)
100
80
60
40
20
0
1
2
3
Session
#
#
#
#
#
#

Figure 4



Chapter 4

General Discussion

Spontaneous behaviors and interactions in two kinds of chimpanzee-chimpanzee situations have been described in the previous two chapters. I begin the general discussion by summarizing the results of these two studies. In the first study, described in Chapter 2, the witness-of-witness who did not see the baiting directly developed tactics to forestall the witness, who had observed the hiding of the food. "Tactic", as used here, refers to flexible deployment of behavior that causes another animal to act to the self's advantage (Byrne, 1995). In several cases, the witness retaliated against those tactics, misleading the witness-of-witness by moving toward an empty container. These episodes may represent examples of deception. Tactics and counter-tactics were developed during interaction between a witness and a witness-of-witness, illustrating the higher social intelligence of chimpanzees. An examination of changes in tactic indicates a possibility that the witness-of-witness understood the witness's knowledge of the location of hidden food. In the second study, described in Chapter 3, 34 of 40 total incidents of observation consisted of the naive chimpanzee observing its experienced partner. Naive chimpanzees observed their partners only after their own failure or before their first attempts, rather than after their own success. Additionally, in 10 cases, naive individuals used the tools left by experienced chimpanzees. Two factors for the transmission of tool use skills were clearly evident: (a) spontaneous observation when necessary for success and (b) enhanced environmental cues given by skilled individuals.

The minimum unit, and basic component, of social interaction is two individuals. The outcomes of such dyadic interactions can be classified into several categories. First, the outcome of an individual's behavior or interaction can be divided into three types: (a) benefit,

(b) loss, and (c) bootlessness (neither benefit nor loss). Then, the outcome of the dyadic situation can be logically classified into the following six categories as shown in Table 1, depending on the outcome for each individual: (1) spitefulness (loss-loss), when both individuals lose; (2) negative-partialness (loss-bootlessness), when one loses and it is bootless for the other; (3) doldrums (bootlessness-bootlessness), when it is bootless for both individuals; (4) opposition (benefit-loss), when one individual benefits and the other loses (this case can be further divided into two categories, "selfishness" and "altruism", depending on whether the benefit is gained by the self or the other, respectively); (5) partialness (benefit-bootlessness), when one individual benefits and it is bootless for the other; and (6) mutualism (benefit-benefit), when both individuals benefit.

<<< Table 1>>>

In each of the first three situational categories listed above, neither individual benefits. Therefore, these cases (spitefulness, negative-partialness and doldrums) cannot be considered representations of the use of social intelligence. In contrast, the latter three categories (opposition, partialness and mutualism) describe cases in which at least one of the two benefits from interaction with the other; social intelligence is expected to operate in exactly such cases. When the studies described in Chapters 2 and 3 are categorized, the study in Chapter 2 is considered an example of "opposition" and that in Chapter 3 an example of "partialness".

In the situation described in Chapter 2, the witness-of-witness benefited, i.e., acquired the hidden banana, after using several tactics against the witness. On the other hand, the witness suffered a loss, as she could not obtain the hidden banana that she would have been able to eat had the witness-of-witness not forestalled her. The witness in pair 1 used deceptive behavior to defend against this loss, or, in other words, to gain the benefit of obtaining the food. The witness-of-witness then developed a counter-tactic to gain access to

the food again. These chains of tactics and counter-tactics can be considered a product of each individual's "selfish" behavior. Overall, this experimental study can be regarded as of the "opposition" type, according to the classification system above.

On the other hand, the situation described in Chapter 2 was bootless for experienced individuals, as they lost nothing by their naive partners observing them. In contrast, naive individuals benefited from observing their experienced partners. Facilitation of the learning of tool use for honey fishing by observing an experienced partner was not confirmed in terms of the speed of acquisition or latency of first success in this study, because the task was too simple for social learning to afford a measurable advantage in acquiring the skill. Considering other studies in the wild and in the laboratory, however, observation of a skilled model does facilitate skill learning (Matsuzawa, 1999; Paquette, 1992; Whiten et al., 1996). In addition, the use of leftover tools observed in the study in Chapter 3 was indeed beneficial for naive chimpanzees. Their success rate with leftover tools was far higher than with their own selection of tools, which included unusable ones. Experienced chimpanzees neither gained nor lost due to partners' use of their leftover tools. Collectively, these results indicate that naive chimpanzees benefited from their experienced partners, whereas the situation was bootless for their experienced partners; thus, the situation can be regarded as an example of "partialness" according to the classification system above.

As mentioned above, "opposition" and "partialness" are two of the three situations in which social intelligence is expected. When multiple individuals compete for limited resources, such as food, mates, and dominance, each individual displays selfish behaviors to gain the resource, resulting in a "opposition" type of situation. Sophisticated social maneuvers can be seen in such situations; one typical example is "deception", as observed in the study in Chapter 2. Byrne & Whiten (1992) examined the distribution of deceptive episodes observed by many different researchers. In order to correct for the amount of time

each species had been studied, they compared the number of deception events with the number of studies per primate taxonomic group. Their work showed that strepsirhine primates, who retain the most primitive traits, have never been seen performing tactical deception; however, the Cercopithecinae and apes have perpetrated a large number of deceptive episodes. In particular, intentional deceptions, i.e., deceptions seemingly accompanied by insight into the mental state of the victim, have been recorded only for great apes. This fact suggests that great apes, unlike other animals, are able to socially manipulate others, using true apprehension of what others know or think. The differences in attributional ability among humans, apes, and monkeys have been ascertained in experimental studies. Chimpanzees discriminate knowledge and ignorance (Povinelli, 1990), while macaques do not (Cheney & Seyfarth, 1990; Povinelli et al., 1992); chimpanzees show empathy, while macaques do not (Povinelli et al., 1992a; b); human children older than four years can attribute false belief to others (Wimmer & Perner, 1983), while three-year-olds and chimpanzees do not (Premack, 1988; Astington, et al.,1988; Premack, 1988; Call & Tomasello, 1999). As for deception, Byrne (1993) found a correlation between Dunbar's (1992) neocortex index and Byrne & Whiten's (1992) frequency of deception records in each primate species, corrected for the amount of observation time per species. The complexity and underlying cognitive mechanisms of social skills thus correspond to the evolutionary stage of each primate species.

A typical example of "partialness" is the social learning situation in the study in Chapter 3; like that of social skills displayed in "opposition" situation, the field of social learning has found differences in levels of cognitive mechanisms according to the evolutionary stage of each primate species. Social learning can be defined as the learning of a behavior, or acquisition of information, through social interaction with other animals. Three main mechanisms of social learning can be distinguished (Thorpe, 1956; Tomasello &

Call, 1997): (a) stimulus enhancement, in which the probability of an animal approaching or contacting something in the environment is increased by seeing another interacting with the same object or place; (b) emulation, in which an animal's "goal" is influenced by watching another's actions; and (c) imitation, in which an animal copies motor actions by observing the behavioral sequence of another. Imitation was once considered a simple process that monkeys and other animals could easily accomplish, but this idea has been refuted (Galef, 1990; 1992). There is no reliable evidence that monkeys truly can imitate or emulate, although stimulus enhancement may be occurring in some cases (Fragaszy & Visalberghi, 1989; Hirata, et al., 2001). On the contrary, great apes show some evidence of imitation and emulation, although even they find it very difficult to imitate (Russon & Galdikas, 1993; Byrne & Russon, 1998; Myowa-Yamakoshi & Matsuzawa, 1998). For example, in the study by Myowa-Yamakoshi & Matsuzawa (1998), five chimpanzees were able to reproduce demonstrated actions on their first try in only 13 out of 240 cases; thus, their rate of imitation by pure observation was 5.4%. Lastly, even as infants, humans are much better than non-human primates at imitating (Meltzoff & Gopnik, 1993). These studies outline the evolutionary stages involved in the area of social learning.

As seen above, the differences of non-human primates' behavior and cognition demonstrated in their social world, as well as those displayed in single subject conditions such as physical causal understanding, and symbolic and numerical comprehension, reflect each species' evolutionary stage (Byrne, 1995; Matsuzawa, 2001). However, the last type of social situation listed above, "mutualism", has not been evaluated in this context; nor have social situations involving more than two individuals. Typical examples representing mutualism are cooperation and division of labor. Cooperation in chimpanzees has been investigated in the laboratory in a few studies (Crawford, 1937; Chalmeau, 1994). Results showed that chimpanzees can coordinate their own actions with others' in order to obtain

otherwise inaccessible food. In the wild, Boesch & Boesch (1989) observed several chimpanzees hunting prey cooperatively, with one group chasing prey in a certain direction and another group waiting for the prey in that direction; such a strategy requires that they cooperate and divide labor during hunting. Examination of behavior and cognition in such mutualistic situations, or in situations involving more than two individuals, is a top priority for further investigation of the evolution and development of primate social intelligence. Overall, comparative studies of behavior and cognition of non-human primates in social situations are indispensable to exploration of the evolution of human intelligence. To date, such studies have been partial to two types: experiments dealing with chimpanzee (monkey)-human pairs, and natural observation of wild (free-ranging) groups of primates. In addition to these two types, we believe that experimental studies dealing with pairs or groups of conspecifics, such as those in Chapters 2 and 3, represent the direction in which cognitive research should advance.

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Acknowledgements

I am deeply grateful to all – people and chimpanzees – who gave me moral and practical support, encouragement, and advice throughout the study.

Table 1. Combinations of the outcomes of two individuals.

Pattern	Combination of the two outcomes	Typical example
Spitefulness	Loss-Loss	
Negative-partialness	Loss-Bootless	
Doldrums	Bootless-Bootless	
Opposition	Benefit-Loss	Deception
Partialness	Benefit-Bootless	Social learning
Mutualism	Benefit-Benefit	Cooperation