The Japanese Journal of Animal Psychology, 57, 1, 29–40 (2007)

Lecture

Competitive and cooperative aspects of social intelligence in chimpanzees

Satoshi Hirata
Great Ape Research Institute, Hayashibara Biochemical Laboratories, Inc.

Abstract Many primate species live in groups with specific social structures. Much attention has been given to the social intelligence hypothesis, which claims that higher cognitive ability is required to survive in a complex than in a simple social world. Here, I describe four sets of studies that investigated social intelligence in captive chimpanzees, including tactical interactions in competition for food, the learning of tool use in a social situation, assisting of infants by mothers, and cooperative problem-solving behavior in an experimental situation. The results illustrate similarities and differences between humans and chimpanzees. Experimental studies using food as a reward tend to emphasize the competitive and selfish nature of chimpanzee behavior, whereas mother-offspring relationships in a non-food context may be a basis for the cooperative aspect of social intelligence.

Intelligence in the social world

Köhler (1925) pioneered the study of intelligence in chimpanzees, the closest living relative of humans. He studied chimpanzee behavior on Tenerife Island at the beginning of the 20th century and focused on the use of various tools such as the positioning of a box on which to step to obtain a banana hanging from the ceiling, the use of a stick to draw food within reach, and the joining of two sticks to make a longer stick. He clearly showed that chimpanzees display "insightful" behavior in many situations. Several decades later, researchers began to study chimpanzees in the wild in Africa and discovered that wild chimpanzees also use tools (e.g., Goodall, 1964), illustrating that the intelligence shown by Köhler in experimentally created situations is actually used in natural situations. We now know that the tool using ability is shared by all species of great apes (chimpanzees, bonobos, gorillas, and orangutans), as they readily use tools especially in captive environments (Tomasello & Call, 1997); regarding tool use in the wild, several cases have been reported for orangutans but only a few cases for the bonobos and gorillas (Breuer, Ndoundou-Hockemba, & Fishlock, 2005; Fox, Sitompul, & van Schaik, 1999; Ingmanson, 1996).

Around the same time as the rise of studies in the wild, chimpanzee language projects began to flourish. Gardner and Gardner (1969) demonstrated that chimpanzees are able to comprehend and produce sign language, and Premack (1971) extended the study to the use of plastic symbols. Rumbaugh (1977) introduced a computerized system and illustrated that chimpanzees understand lexigrams, or artificial symbols, presented on a computer monitor. Matsuzawa (1985) showed that a chimpanzee was able to use Arabic numerals to identify numbers. Another prominent study in captivity focused on self-recognition. Gallup (1970) showed that chimpanzees recognize their reflections in a mirror as themselves; since then, many studies have investigated mirror self-recognition in monkeys and apes (e.g., Anderson, 1999). These studies revealed a clear gap between great apes and other monkeys in

Published online in J-STAGE: May 22, 2007
doi: 10.2502/janip.57.1.1

terms of mirror self-recognition.

At this point, one might argue about the purpose of primate intelligence as demonstrated in captivity. Chimpanzees may be able to understand symbols when taught by humans, but they do not speak human-like language in the wild. They may recognize themselves in a mirror, but they do not encounter mirrors in the wild. Their higher cognitive abilities extracted in experimental situations may not have direct relevance to their lives in the wild. Several hypotheses have been proposed regarding the evolutionary foundation of intelligence. For example, the cognitive map hypothesis states that the necessity for a good representation of the location and timing of food resources within a ranging area is an important factor in the evolution of intelligence (Milton, 1981). The extracted foraging hypothesis posits that the need to forage extractively, i.e., extracting edible parts by cracking nutshells or pulling roots out of the ground, facilitates sensorimotor intelligence (Parker & Gibson, 1977). According to the technical intelligence hypothesis, cognition that enables the hierarchical organization of actions for processing difficult-to-eat food enhances higher cognitive ability (Byrne, 1997). The clambering hypothesis claims that the arboreal lifestyle of great apes is the basis for their self-recognition and tool-using ability because the animals must control their own body and plan their movements to avoid injury from falling (Povinelli & Cant, 1995). The social, or Machiavellian, intelligence hypothesis focuses on the complexity of living in a social world (Humphrey, 1976; Byrne & Whiten, 1988; Whiten & Byrne, 1997). The ability to remember each individual within a group, interacting with group members depending on the individuality of a partner, dealing with friends, and competing with rivals are difficult tasks. Thus, social intelligence plays an important role in their natural lives. In sum, researchers are seeking "natural intelligence" in chimpanzees and other primates.

Of the above mentioned hypotheses, the social intelligence hypothesis has been given much attention, combined with "theory of mind" research in human children (e.g., Tomasello, Call, & Hare, 2003). However, the social intelligence hypothesis alone does not seem sufficient to explain the evolution of intelligence in primates. There are several aspects of primate behavior for which this hypothesis does not appear to explain intelligence (Byrne, 1997). The debate will therefore continue until a consensus is reached.

Here, I do not aim to conclude whether the social intelligence hypothesis is valid. Rather, I revisit actual cases of chimpanzee behavior in social situations to further the understanding of the nature of their social aspects of intelligence.

Deception

Deceptive behavior is one of the most conspicuous features noted when observing wild primates; observers intuitively feel "intelligence" in the natural interactions of primates. Studying deception is difficult, however, because deception should occur rarely. If an individual performs deceptive behavior frequently, this individual will be recognized as a deceiver, as in the story of the boy who cried "wolf," and will fail in accomplishing the deception. Byrne and Whiten (1990) used a method that involved asking numerous researchers to record as many episodes of deception in primates as possible. The authors succeeded in compiling 253 observations of tactical deception in primates. They further identified possible examples of intentional deception; these examples were found much more often among great apes (i.e., chimpanzees, bonobos, gorillas, and orangutans) than among monkeys, suggesting that they have a higher level of social intelligence.

Hirata and Matsuzawa (2001) studied interactions between pairs of adult chimpanzees at the Primate Research Institute, Kyoto University, in an experimentally created competitive situation (see also Hirata, 2006a). The experiment took place in an outdoor chimpanzee enclosure, which measured about 700m^2, and in two indoor rooms. Five containers were set up in the outdoor enclosure. While a pair of female chimpanzees was kept inside, a human experimenter entered the outdoor enclosure and hid a banana in one of the five containers. One of the two chimpanzees was the "witness," who could see where the experimenter hid the banana from a room adjacent to the enclosure through a half-open door. The other chimpanzee was the "witness-of-the-witness," who remained in a second room and could not see the hiding event directly but was allowed a view of the witness observing the outside. The two chimpanzees were released into the enclosure after baiting.

The following is a summary of the results for a pair of chimpanzees, Chloe and Pendesa. The witness-of-the-witness, Pendesa, did not try to find the banana in the initial trials, suggesting that she did not understand the experimental situation at first. After repeated trials, along with the introduction of a series of role reversals, Pendesa seemed to understand the situation better. She began to run ahead of the witness, Chloe, to arrive at the baited location before the witness and obtain the hidden banana. At the same time, the witness began to try to mislead the witness-of-the-witness by taking an indirect route (Figure 1). When the witness-of-the-witness tried to run ahead of the witness, the witness went to an empty container. The witness-of-the-witness actually ran ahead of the witness and began to search the empty container; by this time, the witness had returned to the correct container and found the banana. The witness succeeded in "deceiving" the witness-of-the-witness in a similar manner for a total of four times. However, the witness-of-the-witness developed a counter-deception tactic, and the witness's deception was no longer successful. That is, the witness-of-the-witness remained close by and frequently adjusted her direction to that of the witness so as not to be deceived.

The dominance relationship played an important role in these interactions, as is the case in other aspects of daily interactions in

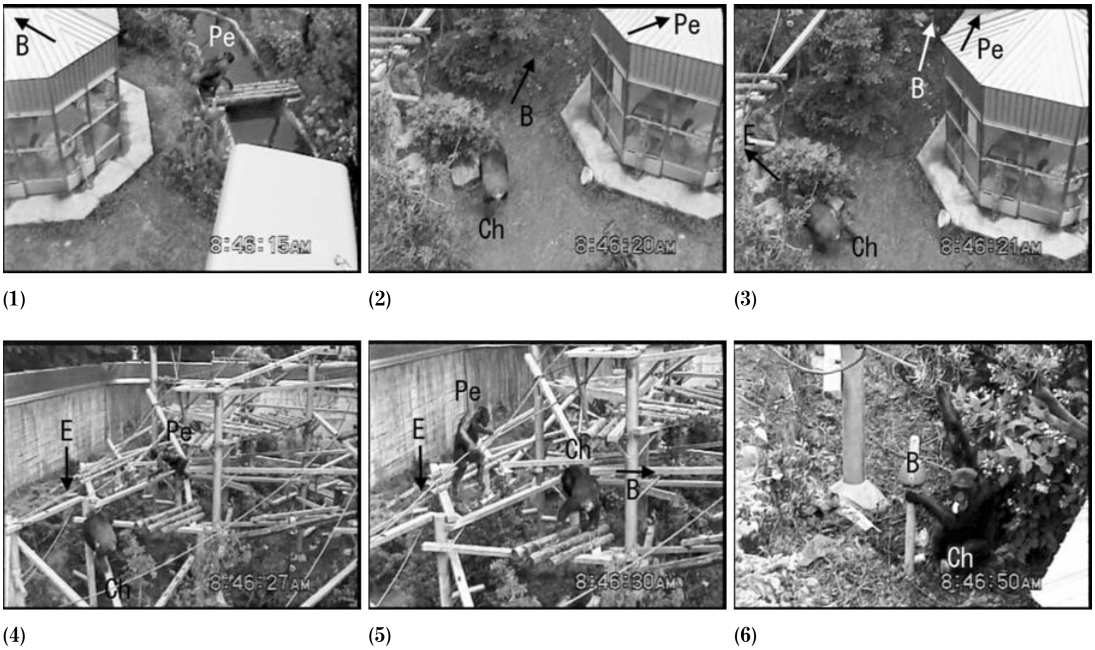

Figure 1. Behavioral sequence of two chimpanzees during the 24th experimental session. (1) The witness-of-the-witness, Pendesa, searching for a hidden banana; (2) the witness, Chloe, going straight for the baited container; (3) Pendesa trying to run ahead of Chloe, who in turn changed her route to an empty container; (4) Pendesa catching up with Chloe about 2 m from the empty container; (5) Pendesa threatening Chloe to chase her away; (6) Chloe obtaining the banana after returning to the baited container while Pendesa checks the empty container. Ch, Chloe; Pe, Pendesa; B, baited container; E, empty container.

captivity or in the wild. Pendesa was dominant over Chloe. Thus, Pendesa, the witness-of-the-witness, had the advantage of being dominant, but at the same time she had the disadvantage of being ignorant about the baited location. In contrast, Chloe had the disadvantage of being subordinate, but had the advantage of knowing the baited location. Such a dilemma produced a situation in which sophisticated maneuvers emerged. It was unclear whether the individuals really intended to deceive the competitor from the beginning of a trial, but it was clear that the competitor was deceived. Both chimpanzees adjusted their own behavior flexibly in response to the rival's tactic.

The above study was based on the pioneering work of Menzel (1974), who observed similar deceptive episodes among captive chimpanzees. Matsuzawa (1991) conducted similar work with chimpanzees at another facility, and the results were similar to those of Menzel (1974). These studies reported a tactic to obtain the hidden food, a deceptive tactic to prevent robbing by misleading the rival to an irrelevant place, and counter-deception to prevent deception. Deceptive episodes tend to be generally anecdotal, as discussed by Whiten and Byrne (1988), but these three cases showed that the deceptive ability of chimpanzees emerges quite reliably under certain experimental situations.

Social learning

Another conspicuous feature of wild chimpanzees is that they learn to use tools and learn other forms of behavior socially from their mothers or other group members (Whiten, Goodall, McGrew, Nishida, Reynolds, Sugiyama, Tutin, Wrangham, & Boesch, 1999). Each chimpanzee group has a different set of behavioral repertoires, or "culture," and an infant born in a group learns the behavioral repertoire specific to that group by closely observing others. Matsuzawa, Biro, Humle, Inoue-Nakamura, Tonooka, and Yamakoshi (2001) used the term "master-apprenticeship" to characterize the chimpanzee cultural process. In this process, a chimpanzee "master" skilled in a certain type of tool use does not actively teach the chimpanzee "apprentice," who is naive in the use of this tool. Rather, through long-term repetitive observation of the master, which is supported by high levels of tolerance on the master's part, including allowing access to tools and food obtained via tool use, the apprentice acquires the skill.

To investigate the chimpanzee master-apprenticeship relationship in more detail, Hirata and Celli (2003) studied the process by which chimpanzee infants learn tool use (see also Hirata 2006b). The targets of the study were three mother-infant pairs at the Primate Research Institute of Kyoto University. The three mothers, Ai, Chloe, and Pan, gave birth in 2000, and all three had already acquired the skill to fish for honey by inserting a slender object into the opening of a honey jar. Hirata and Celli (2003) placed two pairs of mothers and infants together, and observed how the infants learned tool use. They were given eight sets of 20 types of tools scattered on the floor; 12 of these were appropriate tools with which to fish for honey, and the remaining 8 could not be inserted into the honey jar.

From a young age, the infants observed their mothers and other adults repeatedly and carefully (Figure 2a). They observed their mothers, as well as non-related adults, engaging in tool use. When the infants were 1 to 1.5 years old, they began to extend objects toward the honey jars. After the infants reached 1.5 years, they tried to insert objects into the jars with increasing frequency, but their hands were still clumsy and they were unable to complete the task. Although they experienced continual failure, they did not give up, but patiently continued trying. All three infants first succeeded in honey fishing using tools on their own when they were 1 year and 8 months to 1 year and 10 months old. During the process leading up to their first success, they most frequently attempted the task with 2 particular tools of the 20 available tools. These were the tools that the infants had observed being used selectively by the adults. It is likely that the infants learned socially from their mothers and from other models what types of tools should be used.

In this type of situation, human mothers would assist their infants by guiding their

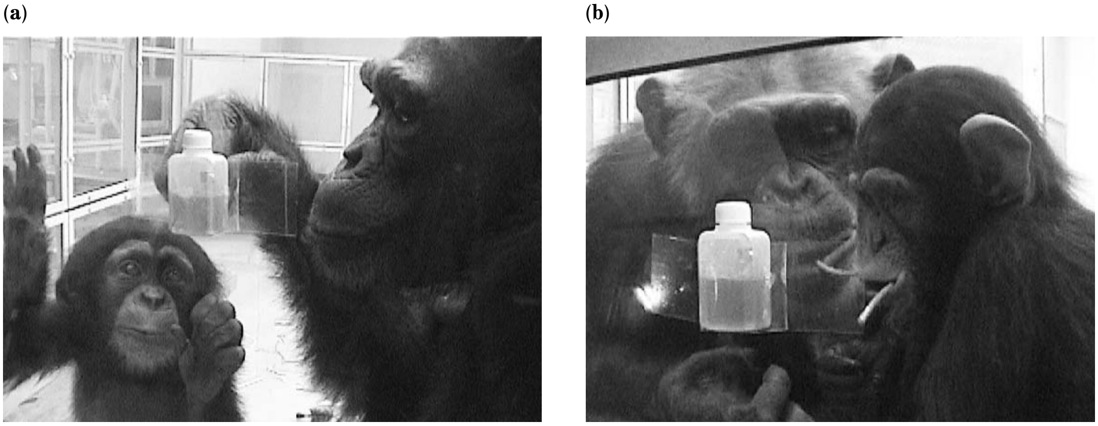

Figure 2. (a) An infant observing her mother and (b) a mother allowing her infant to lick the tool.

hands or verbally encouraging them; they might also perform the task for their babies, providing them with honey. Chimpanzee mothers, however, did not actively teach their offspring in these ways. This is consistent with the previous claim that the chimpanzees generally do not teach others, except for two episodes of observation reported by Boesch (1991). This did not mean that chimpanzee mothers did nothing for their infants; infants often intervened in their mothers' activities by reaching for or trying to steal tools. In these situations, the adult response was twofold: the first was rejection, meaning that adults pushed away the infants' hands to prevent them from reaching for the tools; the second was allowing, whereby the adults allowed the infants to steal tools and sometimes even stopped moving when the infants reach for the tools (Figure 2b). In a few cases, adults offered tools to infants after the infants approached the tools using their hands or mouths. Interestingly, the tools offered by adults to infants almost never had honey on them; mothers only offered a tool to infants after they have already licked the honey from it or before they have used the tool. These results indicate that mothers did not actively offer honey. However, even though the mothers did not teach them, the infants might remain motivated to engage in the same activity as adults by observing the adults, by being allowed to steal a tool, and by occasionally being given a tool. Thus, as Premack and Premack (2003) pointed out, adult tolerance seemed to support infant motivation. The mother-infant interactions observed may represent steps in the evolution of teaching and may constitute an important step in the development of human culture.

Coordination of actions

Cooperation occurs frequently in everyday human lives. Non-human primates also engage in cooperative acts such as cooperative parenting by some species of New World monkeys (Garber, 1997) and reciprocal grooming in many species of monkeys (Muroyama, 1991). With respect to chimpanzees, Boesch and Boesch (1989) described how chimpanzees at Tai, Cote D'Ivoire, hunt their prey cooperatively. Some chimpanzees chase the target, the target runs away, and other chimpanzees wait for the target and capture it. However, whether chimpanzees hunt cooperatively has been debated among researchers (e.g., Gilby, Eberly, Pintea, & Pusey, 2006). Few experimental studies have investigated chimpanzee cooperative abilities (e.g., Crawford, 1937).

Hirata and Fuwa (2007) designed an experiment to test the ability of chimpanzees to cooperate. The subjects were two chimpanzees housed at the Hayashibara Great Ape Research Institute, Okayama, Japan. They presented the two chimpanzees with a task in which they were each required to pull one end of a rope simultaneously to drag blocks supporting food into reach. The chimpanzees did not succeed in the initial tests. They did not immediately understand the necessity for cooperation and they did not adjust their behavior to work with the partner. However, the frequency of success gradually increased as the number of sessions increased and the task was varied. One of the chimpanzees first began to look at the partner frequently, waiting if the partner was not holding the rope, and then pulling the rope in synchrony with the partner. The other chimpanzee also began to perform similar behavior (i.e., glancing at the partner and waiting if necessary) sometime later. Thus, the two chimpanzees learned to coordinate their own behavior with that of the partner, after trial and error. Of note was that they did not use interactive behaviors or eye contact to synchronize their behavior. Both chimpanzees became experienced in this task, and either one could coordinate her behavior to that of the partner, but they did not use mutual eye contact or behavioral signs for the partner to achieve mutual coordination. The absence of interactions may be ascribed to the absence of shared intentionality as suggested by Tomasello, Carpenter, Call, Behne, and Moll (2005).

To further investigate the potential for soliciting behavior, one chimpanzee was then paired with a human partner in the same situation. There were two conditions for the behavior of the partner. In the first condition, the partner approached the rope simultaneously with the chimpanzee and adjusted the timing to pull the rope. In the second condition, the partner delayed the approach and remained still for 2 seconds. When the partner delayed the approach, the experiment resulted in failure in the first several trials. After these initial failures, however, the chimpanzee began to solicit the partner for cooperation by looking up at his face, vocalizing, and taking the partner's hand (Figure 3). When this chimpanzee was again paired with the chimpanzee partner, no soliciting behavior was observed. Communicative behavior emerged during the task, and the communication differed according to the identity of the partner.

In his pioneering work on cooperation in chimpanzees, Crawford (1937) showed that two chimpanzees employed soliciting behaviors to conspecific partners. Gomez (1990) described communicative behavior of a captive gorilla toward a human partner to ask for help in opening a latch. In contrast, Povinelli and O'Neill (2000) wrote that soliciting behavior was not observed between chimpanzees in a cooperative task similar to the Crawford's (1937) study. Further study is needed in terms of necessary condition for the emergence of communicative behavior in cooperative situation.

Melis, Hare, and Tomasello (2006) also investigated cooperation in chimpanzees. They

(a) (b)

Figure 3. (a) A chimpanzee taking a human partner's hand and (b) pulling the string together with the partner.

showed that chimpanzees could recruit a partner to collaborate when necessary, and that they recruited the more effective of two partners on the basis of their past experience with each partner. In another study in the wild, Hockings, Anderson, and Matsuzawa (2006) studied the progression order of a party of chimpanzees when they crossed two man-made roads. The results showed that the progression order was systematically organized, and the authors concluded that dominant chimpanzees act cooperatively with a high level of flexibility to maximize group protection. Thus, researchers are learning more about the level of chimpanzee cooperative ability both in the wild and in captivity.

Assistance

I conducted another observational study of the interactions of the three mother-infant pairs described earlier (Hirata, in press). Chimpanzee infants are born quite helpless. They cannot move by themselves until they are 2 to 3 months old. They begin to walk quadrupedally at around 2 to 3 months of age, but it takes a long time for them to move completely skillfully and independently. This was true for the three infants born at the Primate Research Institute. They were helpless for a while after birth, but gradually moved farther from their mothers as their motor abilities developed, enlarging the area in which they could move by themselves. It was not easy for them, however, to move freely around the enclosures in which they were housed. The enclosures of the Primate Research Institute have a 15 m high metal climbing structure, ropes, platforms at various heights, and planted trees, functionally simulating an African forest. The mothers traveled freely in the enclosures, vertically and horizontally, but the small infants could not do the same.

In such situations, the three mothers were observed communicating with their infants. For example, one mother stretched out her hand toward her offspring who was some distance away from her prior to travel (Figure 4a). The infant then approached its mother to take her hand. The mother cradled the infant and moved from one location to another while carrying her offspring. In another example, a mother poked her infant, who was inches away from her (Figure 4b). The infant responded to this prodding by climbing onto the mother. Maternal behaviors such as stretching out their hands and poking the infant can be recognized as communicative signals toward the infants.

I analyzed these types of behavior of the three mothers and their infants when they began to travel from one location to another in an enclosure when the infants were around 1 to 1.5 years old. Behavioral events that occurred when physical contact was made between mothers and infants who were initially apart could be categorized into three cases. In the first case, called unilateral infant-to-mother contact, the infant caught the mother, but the mother did not show any behavior toward her infant. In the second case, termed unilateral mother-to-infant contact, the mother pulled her infant, but the infant did not show any behavior toward the mother. In the third case, called reciprocal contact, both the mother and her offspring showed some kind of behavior toward each other before their physical contact. In all three pairs, one-third to one-half of the interactions were reciprocal, in which the three mothers and their infants communicated in some way to make physical contact before they traveled together.

The mothers did not necessarily carry their infants when they traveled across the enclosure. They sometimes left the infant and traveled alone. The mothers seemed to judge the situation to decide whether they should carry the infant or travel alone. There were several different cases in which infants had difficulty catching up to their mothers. I examined the relationship between the travel distance and the mothers' behaviors to consider the mothers' judgments depending on different situations. Mothers carried their infants more frequently as the travel distance became longer. Further, I examined the physical contact initiatives by the mothers related to carrying the infants. When the mothers traveled longer distances, they initiated and accomplished physical contact with the infants more often. Thus, it seems that the mothers had already decided on the

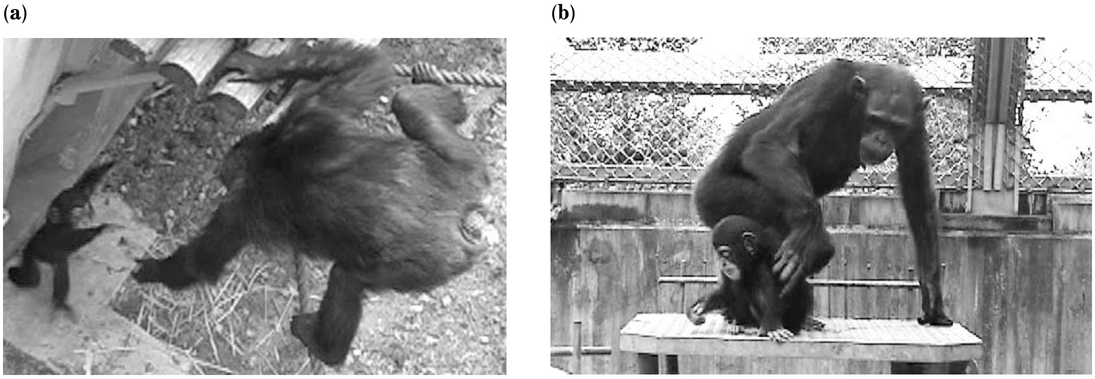

Figure 4. (a) A chimpanzee mother stretching out her hand to her offspring and (b) touching the body of the infant before starting to travel a distance.

destination before they moved. When the destination was far, the mothers initiated contact with their offspring before starting travel, prompting the infant to cling to the mother; the mother and infant then traveled together, and the infant was carried.

The chimpanzee mothers communicated with their infants using several types of behavior, assessed the state of the infants, and planned future behavior taking other individuals into consideration. Infants, on the other hand, understood the behavioral signs of their mothers and responded appropriately. These behaviors can be considered a manifestation of their social intelligence. The mother-infant relationship is the first social relationship that an infant experiences, and the social intelligence of an infant is exhibited in this first social relationship.

Competition and cooperation

In the first study described, two chimpanzees developed tactics and counter-tactics to obtain hidden food. The situation was highly competitive and there was a clear distinction between the winner and loser; the winner obtained food, whereas the loser did not. In theory, the chimpanzees could have shared the food, but they never did. If their behaviors were to be categorized as either selfish or altruistic, they would be considered selfish. Their intelligence was used to compete with the rival.

In the second study, in which social learning to obtain honey took place, the situation was not highly competitive. The infants benefited by observing their mothers and learning a skill. The mothers generally did not lose much as a result of the infants' activities. Whereas the mothers were sometimes tolerant to the infants who was stealing the tools that they were using, they were not truly altruistic toward their infants in this situation. When the mothers actively gave tools to the infants, they did so after licking the tools themselves or before they inserted the tool into the honey. Thus, they did not actively give honey to the infants. Another thing to note was the absence of teaching, which can be defined as a type of behavior that is costly or does not provide any immediate benefit for the teacher, but benefits the pupil through knowledge acquisition or skill learning (Caro & Hauser, 1992). In sum, chimpanzee masters behave as a model without teaching the apprentices, and apprentices learn by repeatedly observing the masters.

In the third study, two chimpanzees pulled both ends of a rope simultaneously to obtain food. If cooperation is defined as two individuals acting together to reach a common goal (Boesch & Boesch 1989), then the behavior of these two chimpanzees would be considered cooperative because they coordinated their behavior to obtain the blocks supporting food that they could not otherwise reach. However, cooperation in the common sense may refer to a behavior whereby an individual actively assists or supports others, with costs to the actor and benefits to the receiver (van Schaik & Kappeler 2006). The task performed here did not impose costs on the partners; rather, both benefited by obtaining food. Thus, their behavior may not be considered cooperative from this perspective. Furthermore, they may have been using the partner as a “tool” to achieve their own goal. When the partner was a conspecific, they checked the behavior of the partner, waited, and adjusted their behavior; when the partner was human, the chimpanzee solicited the partner to work with her. In both cases, the behavior of the partner was used to achieve their own goal. Therefore, the way in which the chimpanzees behaved in this situation is slightly different from the case in which two individuals help each other, as humans do in their daily lives.

In the last study, the mothers communicated with their infants when they traveled. The ultimate goal of the behavior of the mothers may be to increase their reproductive success. Because the infants of great apes and humans are especially helpless and develop very slowly (Purvis, Webster, Agapow, Jones, & Isaac, 2003), the need for maternal care is great. The infants thus require help from their mothers, and mothers need to help infants move. To ensure the reproductive success of mothers and survival of infants, it is important to have clear communication to coordinate traveling together, depending on the situation. From this perspective, this example may be viewed as selfish behavior. The ultimate reason for their communication can be considered as such, but from a proximate view, the situation can be described as mothers “helping” their immature infants when the infants were not able to move freely on their own. Mother-infant interactions of a similar kind have been reported in studies of orangutans, chimpanzees, and gorillas (Bard, 1992, 1994; Whiten, 1999). From a proximate view, I consider these parenting behaviors to be altruistic toward the infants.

Rivals, friends, and parent-offspring

As the Machiavellian intelligence hypothesis explains, living in a social world is a difficult task. Food resources are limited within a habitat in which a group lives, and the limited number of males and females within a group means that mating resources are also limited. Hare (2001) argued that group-living primates are constantly competing against conspecifics for access to food and mates, and it thus follows that selection has favored individuals capable of out-competing conspecifics. Tomasello et al. (2003) similarly claimed that chimpanzee cognitive skills are shaped under competitive pressure among conspecifics. Indeed, Hare and Tomasello (2004) showed that chimpanzees performed more skillfully when competing than when cooperating in different types of cognitive tasks.

There is likely some truth to these claims. Winning in competition over food and mating resources is very important for survival and reproduction. As described above, chimpanzees used the behavior of another individual to gain benefits for the self in the study of deception (Hirata & Matsuzawa, 2001), in the social learning of tool use (Hirata & Celli, 2003), and even in a cooperative task (Hirata & Fuwa, 2007). However, it is also true that they are not always competing with other group members in their natural group lives. They travel together, play together, and groom each other. In addition, the arrangements of experimental studies should be considered carefully. Researchers tend to use food as a reward to facilitate or elicit the behavior of subject animals in experimental manipulations, as did Hare and Tomasello (2004) in their comparative study of cooperative and competitive behavior in chimpanzees. In many cases, using food rewards is an effective way to investigate the potential capabilities of animals. However, food may become an obstacle in some cases. Segerdahl, Fields, and Savage-Rumbaugh (2005) described that using food as a reward inhibits, rather than stimulates, the spontaneous behavior of apes. These authors carefully explained a process by which a male bonobo named Kanzi acquired language, and they indicated that giving a food reward became complicated and food became a problem in the interactions with the apes during the initial stages before they recognized that Kanzi had learned language spontaneously. They further reported that the presence of food made Kanzi's attention to the situation one-directional.

The presence of food may make a situation competitive; consequently, the competitive nature of intelligence predominates in such situations. In other words, primates may become friends, rather than rivals, in a non-food-related context. Hockings et al. (2006) showed that chimpanzee cohesiveness increased in dangerous situations, and chimpanzees engaged in a division of labor to protect the group. Thus, they behaved altruistically and cooperatively in a non-food context. The mother-offspring relationship is notable in this respect, at least in chimpanzees, because the most frequent contact that occurs in a non-food context would involve mother-infant pairs due to the infants' long dependency on their mothers. Hirata (in press) showed that mother and infant chimpanzees communicated frequently in situations in which the mothers needed to assist the infants during travel. While competitive aspects of social intelligence play an important role when interacting with rivals against limited resources, cooperative and altruistic aspects of social intelligence may have been fostered in mother-offspring relationships during the evolutionary pathway of primates.

References

Anderson, J. R. (1999). Primates and representations of self. Current Psychology of Cognition, **18**, 1005–1029.

Bard, K. A. (1992). Intentional behavior and intentional communication in young free-ranging orangutans. Child Development, **63**, 1186–1197.

Bard, K. A. (1994). Evolutionary roots of intuitive parenting: maternal competence in chimpanzees. Early Development and Parenting **3**, 19–28.

Boesch, C. (1991). Teaching among wild chimpanzees. Animal Behaviour, **41**, 530–532.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. American Journal of Physical Anthropology, **78**, 547–573.

Breuer, T., Ndoundou-Hockemba, M., & Fishlock, V. (2005). First observation of tool use in wild gorillas. PLoS Biology, **3**, 2041–2043.

Byrne, R. W. (1997). The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? In A. Whiten and R. W. Byrne (Eds.), Machiavellian Intelligence II: Extensions and Evaluations (pp. 289–311). Cambridge, UK: Cambridge University Press.

Byrne, R. W., & Whiten, A. (1988). Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans. Oxford, UK: Clarendon Press.

Byrne, R. W., & Whiten, A. (1990). Tactical deception in primates: the 1990 database. Primate Report, **27**, 1–101.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman primates? Quarterly Review of Biology, **67**, 1511–174.

Crawford, M. P. (1937). The cooperative solving of problems by young chimpanzees. Comparative Psychology Monographs, **14**, 1–88.

Fox, E. A., Sitompul, A. F., & van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In: S. T. Parker, R. W. Mitchell, H. L. Miles (Eds.) The mentalities of gorillas and orangutans: Comparative perspectives (pp 99–116). Cambridge, UK: Cambridge University Press.

Gallup, G. G. (1970). Chimpanzees: self-recognition. Science, **167**, 86–87.

Garber, P. (1997). One for all and breeding for one: cooperation and competition as a tamarin reproductive strategy. Evolutionary Anthropology, **5**, 187–199.

Gardner, R. A., & Gardner, B. T. (1969). Teaching sign language to a chimpanzee. Science, **165**, 664–672.

Gilby, I. C., Eberly, L. E., Pintea, L., & Pusey, A. E. (2006). Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*. Animal Behaviour, **72**, 169–180.

Gomez, J. C. (1990). The emergence of intentional communication as a problem-solving strategy in the gorilla. In: S. T. Parker & K.

R. Gibson (Eds.) "Language" and intelligence in monkeys and apes: comparative developmental perspectives (pp 333–355). New York: Cambridge University Press.

Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. Nature, **201**, 1264–1266.

Hare, B. (2001). Can competitive paradigms increase the validity of experiments on primate social cognition? Animal Cognition, **4**, 269–280.

Hare, B., & Tomasello, M. (2004). Chimpanzees are more skillful in competitive than in cooperative tasks. Animal Behaviour, **68**, 571–581.

Hirata, S. (2006a). Tactical deception and understanding of others in chimpanzees. In: T. Matsuzawa, M. Toimonaga, & M. Tanaka (Eds.), Cognitive Development in Chimpanzees (pp 265–276). Tokyo: Springer-Verlag.

Hirata, S. (2006b). Learning and transmission of tool use to fish for honey in chimpanzees. In: T. Matsuzawa, M. Toimonaga, & M. Tanaka (Eds.), Cognitive Development in Chimpanzees (pp 201–213). Tokyo: Springer-Verlag.

Hirata, S. (in press) Communication between mother and infant chimpanzees and its role in the evolution of social intelligence. In: K. Fujita & S. Itakura (Eds.) Origins of the Social Mind: Evolutionary and Developmental Views. Tokyo: Springer-Verlag.

Hirata, S., & Celli, M. L. (2003). Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. Animal Cognition, **6**, 235–244.

Hirata, S., & Fuwa, K. (2007). Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. Primates, **48**, 13–21.

Hirata, S., & Matsuzawa, T. (2001). Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). Animal Cognition **4**, 285–295.

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road-crossing in chimpanzees: a risky business. Current Biology, **16**, 668–670.

Humphrey, N. K. (1976). The social function of intellect. In: P. P. G. Bateson, & R. A. Hinde (Eds.), Growing Points in Ethology (pp 451–479). Cambridge, UK: Cambridge University Press.

Ingmanson, E. J. (1996). Tool-using behavior in wild Pan paniscus social and ecological considerations. In: A. E. Russon, K. A. Bard, S. T. Parker (Eds.) Reaching into thought: the minds of the great apes (pp 190–210). New York: Cambridge University Press.

Köhler, W. (1925). The Mentality of Apes. New York: Harcourt Brace.

Matsuzawa, T. (1985). Use of numbers in a chimpanzee. Nature, **315**, 57–59.

Matsuzawa, T. (1991). Chimpanzee Mind (in Japanese). Tokyo: Iwanami-Shoten.

Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2001). Emergence of culture in wild chimpanzees: education by master-apprenticeship. In: T. Matsuzawa (Ed.) Primate Origins of Human Cognition and Behavior (pp 557–574). Tokyo: Springer-Verlag.

Melis, A. P., Hare, B., & Tomasello, M. (2006). Chimpanzees recruit the best collaborators. Science, **311**, 1297–1300.

Menzel, E. W. (1974). A group of chimpanzees in a one-acre field. In: A. M. Shrier, & F. Stollnitz (Eds.) Behavior of Non-Human Primates, volume 5 (pp 83–153). San Diego: Academic Press.

Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. American Anthropologist, **83**, 534–548.

Muroyama, Y. (1991). Mutual reciprocity of grooming in female Japanese macaques (*Macaca fuscata*). Behaviour, **119**, 161–170.

Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. Journal of Human Evolution, **6**, 623–641.

Povinelli, D., & Cant, J. G. H. (1995). Arboreal clambering and the evolution of self conception. Quarterly Review of Biology, **70**, 393–421.

Povinelli, D. J. & O'Neill, D. (2000). Do chimpanzees use their gestures to instruct each other? In: S. Baron-Cohen, H. Tager-Flusberg, & D. Cohen (Eds.) Understanding other minds: perspectives from developmental cognitive neuroscience, 2nd edn (pp 459–487). Oxford: Oxford University Press.

Premack, D. (1971). Language in a chimpanzee? Science, **172**, 808–822.

Premack, D., & Premack, A. (2003). Original Intelligence: Unlocking the Mystery of Who We Are. New York: McGraw-Hill.

Purvis, A., Webster, A. J., Agapow, P., Jones, K. E., & Isaac, N. J. B. (2003). Primate life histories and phylogeny. In: P. M. Kappeler, & M. E. Pereira (Eds.) Primate Life Histories and Socioecology (pp 25–40). Chicago: University of Chicago Press.

Rumbaugh, D. M. (1977). Language Learning by a Chimpanzee: The Lana Project. New York: Academic Press.

Segerdahl, P., Fields, W., & Savage-Rumbaugh, S. (2005). Kanzi's Primal Language: The Cultural Initiation of Primates into Language. Hampshire, UK: Palgrave Macmillan.

Tomasello, M., & Call, J. (1997). Primate cognition. New York: Oxford University Press.

Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees understand psychological states-the question is which ones and to what extent. Trends in Cognitive Science, **7**, 153–156.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. Behavioral and Brain Sciences, **28**, 675–690.

van Schaik, C. P., & Kappeler, P. M. (2006). Cooperation in primates and humans: closing the gap. In: C. P. van Schaik, & P. M. Kappeler (Eds.) Cooperation in Primates and Humans: Mechanisms and Evolution (pp 3–21). Berlin: Springer-Verlag.

Whiten, A. (1999). Parental encouragement in gorilla in comparative perspective: implications for social cognition and the evolution of teaching. In: S. T. Parker, R. W. Mitchell, & H. L. Miles (Eds.) The Mentalities of Gorillas and Orangutans (pp 342–366). Cambridge, UK: Cambridge University Press.

Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. Behavioural and Brain Sciences, **11**, 233–273.

Whiten, A., & Byrne, R. W. (1997). Machiavellian Intelligence II: Extensions and Evaluations. Cambridge, UK: Cambridge University Press.

Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiayama, Y., Tutin, C., Wrangham, R., & Boesch, C. (1999). Culture in chimpanzees. Nature, **399**, 682–685.

（2007．２．１ 受稿，2007．４．14 受理）