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REVIEW ARTICLE

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Chimpanzee social intelligence: selfishness, altruism, and the mother–infant bond

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Abstract To better understand the human mind from an evolutionary perspective, a great deal of research has focused on the closest living relative of humans, the chimpanzee, using various approaches, including studies of social intelligence. Here, I review recent research related to several aspects of social intelligence, including deception, understanding of perception and intention, social learning, trading, cooperation, and regard for others. Many studies have demonstrated that chimpanzees are proficient in using their social intelligence for selfish motives to benefit from their interactions with others. In contrast, it is not yet clear whether chimpanzees engage in prosocial behaviors that benefit others; however, chimpanzee mother–infant interactions indicate the possibility of such behaviors. Therefore, I propose that chimpanzees possess rudimentary traits of human mental competence not only in terms of theory of mind in a broader sense but also in terms of prosociality involving regard for others. Mother–infant interactions appear to be particularly important to understanding the manifestation of social intelligence from an evolutionary perspective.

Keywords Chimpanzees · Mother–infant relationship · Social intelligence · Theory of mind

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Introduction

Three decades have passed since Premack and Woodruff (1978) coined the phrase "theory of mind." Developmental psychological studies of human children have since used this paradigm to document how children understand each other's minds in terms of beliefs, desires, and knowledge (e.g., Wimmer and Perner 1983; Baron-Cohen et al. 1985). This new paradigm also created a basis for the comparative study of social cognition in nonhuman primates from an evolutionary perspective. After the concept of "Machiavellian intelligence" was introduced (Byrne and Whiten 1988), researchers began to increasingly discuss its relation to primates, in terms of the theory of mind and other types of social cognition (e.g., Whiten and Byrne 1997).

Call and Tomasello (2008) summarized recent advances in the study of chimpanzees' understanding of the minds of other individuals. They concluded that chimpanzees understand others in terms of a perception–goal psychology but not in terms of full-fledged, human-like belief–desire psychology. In other words, chimpanzees have a theory of mind in a broad sense, yet they do not possess a more narrowly defined theory of mind that requires understanding of false beliefs. Therefore, although chimpanzees lack certain human traits, humans do not possess an entirely unique social intelligence; rather, some rudimentary traits exist in chimpanzees (Call and Tomasello 2008).

However, Premack (2007) offered a different view. According to his summary, recent results in the field of brain science point to a human singularity in brain structure that is located in areas associated with complex social cognition (theory of mind) or language; in contrast, a number of animal cognition studies appear to indicate similarities between humans and nonhuman animals. Yet, after examining eight cognitive cases (i.e., teaching, short-term

memory, causal reasoning, planning, deception, transitive inference, theory of mind, and language), Premack (2007) claimed that similarities between humans and animals are small and concluded that both brain and cognitive studies highlight the disparities between the human and nonhuman animal.

Here, I reconsider aspects related to social cognition in chimpanzees with reference to recent findings. First, I briefly review results of research into social intelligence, ranging from selfish deception to altruistic behavior. Second, I outline important issues in this field along with my personal observations, emphasizing the mother–infant relationship; although several of my observations are unpublished "anecdotes," they may help elucidate points for future theoretical and empirical research.

Deception

Deceptive behavior is one of the most conspicuous actions noted when observing nonhuman primates; in particular, observers intuitively feel "intelligence" in the deceptive interactions of primates. Byrne and Whiten (1990) compiled 253 reported observations of tactical deception in primates and identified possible examples of intentional deception, which occurred more often among great apes than among monkeys, suggesting a higher level of social intelligence in apes.

During an experimental study, Hirata and Matsuzawa (2001) observed deceptive "misleading" behaviors when chimpanzees attempted to obtain a banana hidden in an enclosure (see also Hirata 2006a). While the subordinate "witness," who had seen where the experimenter had hidden the banana, initiated an approach to the hiding place, the dominant "witness-of-the-witness," who had not directly seen the hiding event, began to run ahead of the witness. At the same time, the witness began to try to mislead the witness-of-the-witness by going to an area where there was no banana. When the witness-of-the-witness tried to run ahead of the witness and began to search the empty area, the witness returned to the correct location and found the banana. This study was based on the pioneering work of Menzel (1974), who observed similar deceptive episodes among captive chimpanzees. Matsuzawa (1991) conducted comparable chimpanzee research at another facility and obtained results similar to those of Menzel (1974). As discussed by Whiten and Byrne (1988), deceptive episodes tend to be anecdotal, but the above three cases indicate that the deceptive ability of chimpanzees emerges quite reliably under certain experimental conditions.

Hare et al. (2006) experimentally explored another aspect of deception in chimpanzees: deception by concealment. In their study, a human experimenter competed against chimpanzees for food. If the human saw a chimpanzee approaching a piece of food, then the human retrieved the food. In response, chimpanzees approached the food from the side that the human was not facing or from the side with an opaque barrier between the chimpanzees and the human, highlighting their ability to deceive by concealment. Moreover, chimpanzees used a tactic of indirect approach by initially distancing themselves from the food while in view of the human and then approaching the food later when behind the human or the barrier (Hare et al. 2006). Overall, these results support the view that chimpanzees know what others can and cannot see.

Understanding of perception and intention

The above examples of deception reinforce the notion that chimpanzees understand the visual perception of others. In a series of experiments with chimpanzees, Hare et al. (2000, 2001) and Bräuer et al. (2007) more explicitly tested these abilities. With several variations, the basic set-up of their experiments included a dominant and subordinate pair facing pieces of food which the dominant individual could or could not see, had been shown or had not been shown, or did or did not know about. If the subordinate individual understood the visual perspective of the dominant, he/she would approach a piece of food that the dominant could not see, had not seen, or did not know about, in order to avoid conflict over food with the dominant. The results supported the theory that subordinate individuals understand the visual perspective of dominant individuals.

In addition to understanding what others can and cannot see, researchers have investigated whether chimpanzees comprehend the goals of the actions of others (Call and Tomasello 1998; Call et al. 2004; Myowa-Yamakoshi and Matsuzawa 2000; Tomasello and Carpenter 2005). In these studies, the responses of chimpanzees were recorded after they observed an actor performing an action that did not meet the actor's intended goals, such as unsuccessful attempts at object manipulations. The results of these studies collectively indicated that chimpanzees understand the goals or intentions of others.

Social learning and the absence of active teaching

Whether in the wild or in captivity, an individual will often benefit from the behaviors of others in a social learning context. Wild chimpanzees socially learn to use tools and learn other forms of behavior from their mothers or other group members (e.g., McGrew 1992). Numerous studies in

nature and in captivity have investigated phenomena involving social learning. Whereas observations in the wild have demonstrated the existence of culture among chimpanzees (e.g., Whiten et al. 1999), studies in captivity suggest that true imitation is more difficult for chimpanzees than was initially thought (e.g., Myowa-Yamakoshi and Matsuzawa 1999). However, research in captivity has begun to reveal social features of chimpanzees, such as conformity to the group norm and traditions over generations (Hopper et al. 2007; Horner et al. 2006; Whiten et al. 2005, 2007), all of which support the theory of "culture" among wild populations in Africa.

In contrast to their excellent ability to learn socially, an intriguing fact is that chimpanzees lack active teaching. For example, in three mother–infant pairs, Hirata and Celli (2003) studied the process by which chimpanzee infants learn tool use in the presence of skilled mothers (see also Hirata 2006b). Infants repeatedly and carefully observed their mothers and other adults and mastered tool-use behavior after the spontaneous observation of successful performances by other individuals. However, there were no cases that could be interpreted as active teaching by a mother. The mothers never exhibited key active-teaching behaviors, such as guiding the infants' hands or performing the task for their babies.

Matsuzawa et al. (2001) used the term "master apprenticeship" to characterize the chimpanzee cultural process. During this process, a chimpanzee "master," who is skilled in a certain type of tool use, does not actively teach the chimpanzee "apprentice," who is naïve in the use of this tool. Rather, through long-term repetitive observations of the master that are supported by high levels of tolerance by the master (e.g., allowing access to tools and to food obtained via tool use), the apprentice acquires the skill.

Trading and role-taking

An individual may also benefit through interacting with others by engaging in trading. Trading in nonhuman primates has become the focus of recent studies under the framework of the biological market (Noë 2001), in which individuals use mental capacity to exchange currency, such as grooming and support for other group members, in a social market (i.e., their group). In Kanyawara, Uganda, Duffy et al. (2007) reported a positive correlation between mating success in wild chimpanzee males and their level of support of the alpha male, indicating that the alpha male in this group selectively tolerated mating by his allies and exchanged mating tolerance for support in conflicts. In another group of wild chimpanzees at Bossou, Guinea, Hockings et al. (2007) examined sharing of cultivated plant foods among group members. In this group, sharing primarily consisted of adult males sharing with reproductively cycling females by offering exchanges of food for mating or grooming.

Another interesting phenomenon has been observed within the complex social network of wild chimpanzees at Bossou. When chimpanzees at Bossou encounter the road that cuts through their home range, they typically do not cross alone but gather at a certain spot in the bushes along the road and march in parade. Crossing the roads is risky, because they have to leave the forest and enter open areas where they encounter humans and vehicles. Hockings et al. (2006) examined the progression order of parties of chimpanzees crossing the roads. Typically, the second-ranking male scanned the road, the first-ranking male took the rearmost position, and females and young individuals occupied the more protected middle positions. Thus, the males engaged in role-taking activity in this situation. Hockings et al. (2006) concluded that dominant chimpanzees act cooperatively with a high level of flexibility to maximize group protection.

Cooperation

As indicated in the example above, chimpanzees may cooperate with each other. Boesch and Boesch (1989) suggested that chimpanzees at Taï, Côte d'Ivoire, hunt their prey cooperatively. Several chimpanzees chase the target, and when the target runs away, several other chimpanzees lie in wait to capture it. However, cooperative hunting in chimpanzees has been debated (e.g., Gilby et al. 2006).

Several experimental studies have tested cooperative ability in captive individuals, demonstrating that two chimpanzees were able to act together to pull a heavy box to obtain food (Crawford 1937) or to pull a handle to make food fall from a dispenser (Chalmeau 1994). Similar experimental studies have been recently revisited. Povinelli and O'Neill (2000) used a method identical to that of Crawford (1937) to investigate whether an individual who had mastered the skill necessary for a task would instruct a naïve partner; however, they found no such evidence. Hirata and Fuwa (2007) designed a new task in which two chimpanzees were each required to pull one end of a rope simultaneously to drag blocks supporting food into reach (see also Hirata 2007; Hirata et al. in press). The chimpanzees did not succeed during initial tests, in that they did not immediately understand the necessity for cooperation and did not adjust their behavior to work with the partner. However, in subsequent tests, the frequency of success gradually increased. Thus, the two chimpanzees learned to coordinate their own behavior with that of the partner by watching the partner and waiting if necessary.

Interestingly, the chimpanzees did not use mutual eye contact or behavioral signs to achieve mutual coordination (Hirata and Fuwa 2007; but see Crawford, 1937). Melis et al. (2006a) used an experimental method that was fundamentally identical to the task described above. They demonstrated that (a) chimpanzees could recruit a partner to collaborate only when necessary, and (b) they recruited the more effective of two partners for collaboration on the basis of their past experience with each partner, concluding also that tolerance plays an important role in chimpanzee cooperative actions (Melis et al. 2006b).

Altruism and regard for others

The step beyond cooperation is altruism or regard for others. Warneken et al. (2006, 2007) and Warneken and Tomasello (2006) explored altruism in chimpanzees in a series of experiments in which chimpanzees observed a human trying to reach an object or another chimpanzee trying to open a door. Their results offered evidence for altruistic behavior, as the chimpanzees helped conspecifics to open the door and both familiar and unfamiliar humans to reach an object.

In contrast, other experimental studies have found negative evidence for altruism. Silk et al. (2005), Vonk et al. (2008), and Jensen et al. (2006) investigated whether chimpanzees would provide food to other group members. In these studies, the chimpanzees could choose whether to provide a food reward only to themselves or simultaneously to themselves and another member of the group. Results consistently indicated that chimpanzees would not offer food to the other group members. Silk et al. (2005) concluded that chimpanzees are indifferent to the welfare of group members.

An interim summary: predominance of selfish motives?

The above research into the social intelligence of chimpanzees indicates that they are skillful at interacting with others in various ways, but their primary motivations are selfish. For example, these experiments have clearly demonstrated selfish motives during interactions such as deception, social learning, and trading. Chimpanzees seek benefits by deceiving other individuals in competitive situations and by observing a skilled master in social learning situations, and they expect future benefits when engaging in trading. Moreover, chimpanzees solve even cooperative tasks for selfish motives, in that they work together with partners because they selfishly desire the resulting food reward. Indeed, in an experimental study, Hirata and Fuwa (2007) never observed chimpanzees helping partners to obtain food (see also Hirata et al. in press). In addition, chimpanzees lack active teaching in social learning situations, which supports the hypothesis that they are indifferent to the benefits of others. Furthermore, Vonk et al. (2008) suggested that the results of Warneken et al. (2006, 2007) can also be interpreted from a selfish perspective, as chimpanzees may help others in expectation of obtaining future rewards.

The above interpretation is in concert with the view of Tomasello et al. (2005), that apes lack shared intentionality. According to their description, shared intentionality consists of understanding the goals, intentions, and perceptions of another individual, along with a motivation to share these things in interaction with others; that is, "we" intentionality. The predominance of selfish motives described in the above paragraph may be linked to the absence of motivation to share intentionality, as proposed by Tomasello et al. (2005). Chimpanzee behaviors in many situations are caused not by "we" intentionality but by "me" desire.

However, is it really the case that chimpanzees only act cooperatively for selfish motives? Predominance of selfish motives does not necessarily mean absence of shared intentionality. If there is a situation in which the chimpanzees' selfish motive is diminished, then they may show truly cooperative behaviors or other-regarding behaviors. The predominance of selfish motives is not entirely synonymous with the hypothesized lack of "we" intentionality. Vonk et al. (2008) briefly noted that other-regarding sentiments are not activated when food is present, because food is an object of competition. In addition to this possibility, my own experience has revealed other complications related to testing chimpanzees in experimental situations. I conduct touch-screen tasks with chimpanzees at the Hayashibara Great Ape Research Institute (Hirata, unpublished data). If a chimpanzee solves a task by touching the touch screen, he/she can receive a food reward. The touch-screen tasks are conducted in two locations: an outdoor booth in an open enclosure and an indoor experimental booth. Interestingly, the motivations of chimpanzees differ greatly between these two locations. When a task is performed in the outdoor booth, it is completed very easily; a 1–2-g piece of apple is a sufficient reward for a successful trial, and chimpanzees repeat the task for >200 trials (sometimes >2000 trials) with no problems. In contrast, when chimpanzees are taken individually to the indoor experimental booth, they all become reluctant to perform the same task. Even if I offer one-eighth of an apple (approximately 30 g) for a successful trial, chimpanzees often exhibit a gesture of refusal. Thus, even if the basic structure of the task remains the same (i.e., a certain behavior results in a food reward), differences in the environment that seemingly have no direct relationship to the task itself greatly alter the attitude

of the chimpanzees (see also Hirata 2006a). Thus, it is incorrect to naïvely presume that a food reward can induce any type of behaviors that a chimpanzee has the potential to perform in any circumstances. The failure to create a situation in which chimpanzees will behave a certain way does not necessarily mean that the animals lack an ability to behave in that manner. As de Waal (in press) pointed out, absence of evidence does not mean evidence of absence.

Regard for others and the mother–infant relationship

In this second part of the paper I offer my observations of chimpanzees, accompanied by illustrative anecdotes, to rethink the possibility of other-regarding behaviors that cannot be interpreted solely as products of selfish motives.

Food and object sharing

Regarding the conclusion of Vonk et al. (2008) that chimpanzees do not actively offer food, I present a case of food sharing. Vonk et al. (2008) referred to a claim that food exchange in chimpanzees is better described as "tolerated theft" than voluntary sharing, or that it can be explained by calculated self-interest to gain benefits in later interactions. However, these explanations appear to be unsatisfactory in some cases of food sharing, the most frequent type of which occurs between mothers and infants. Ueno and Matsuzawa (2004) quantitatively analyzed food sharing in three mother–infant pairs of captive chimpanzees and determined that mothers generally do not offer preferable parts of food material to their infants. Therefore, in many cases, food sharing between the chimpanzee mother and infant does not involve the mother offering preferred foods to the infant. However, other cases exist in which a mother actively offered a preferred food item to the infant following the infant's begging (see Fig. 1). The active offering of food by the mother appears to imply something beyond just "tolerated theft." In addition, mothers do not expect anything in return from the young infant; thus, it is difficult to interpret such cases as calculated self-interest.

Hirata and Celli (2003) observed offerings of a tool by mothers to their infants during the process by which infants learn tool use to fish for honey. In such cases, the tools offered by adults to infants almost never had honey on them; mothers only offered a tool to infants after they had already licked the honey from it or before they had used the tool. Therefore, mothers generally did not offer a reward to the infant. However, the mothers sometimes did not merely allow the infants to take the tool from their hands, but they actively offered tools to infants (see Fig. 2). The tolerated theft hypothesis seems insufficient to explain the active behavior of the mothers, and these behaviors of the mothers cannot be explained as calculated self-interest, as in the case of food sharing between mothers and infants.

Fig. 1 A chimpanzee mother offering one of her favorite food items (sweet potato) to her infant from mouth to mouth

Fig. 2 A chimpanzee mother giving a tip of a tool to her infant to fish for honey

Instead, active food or object sharing may constitute a step toward human-like regard for others. As these cases most often occur between the mother and infant, the mother–infant bond may have provided a rudimentary basis for the evolution of other-regard or altruism.

Teaching by inhibition

According to Premack (2007), teaching in humans is completely different from teaching in nonhuman animals. Teaching in humans is a domain-general competence based on theory of mind, whereas teaching in animals, such as a cat injuring mice and bringing them to her kittens, is an adaptation targeted to a single goal. Chimpanzees generally do not actively teach others. For example, Hirata and Celli

(2003) conducted detailed observations of mothers and infants during situations in which infants learn tool use, and there were no instances of active teaching.

While teaching by encouragement (i.e., encouraging another individual to do something) has not been observed in chimpanzees, except for the observations by Boesch (1991), teaching by inhibition (i.e., preventing another individual from doing something) has been reported on several occasions. For example, when wild chimpanzee infants approach a plant that is not included in the diet of the population, the mothers pull the infants away from the plant (Hiraiwa-Hasegawa 1990), and this action can be interpreted as an example of teaching by inhibition. I have observed several cases that can be classified as teaching by inhibition in a mother–infant pair at the Hayashibara Great Ape Research Institute. For experimental purposes, several nut-cracking sites consisting of an anvil and hammer stones have been created in an open enclosure. The hammer stones are fixed to the ground by a stainless steel chain to prevent the chimpanzees from moving or throwing them away. When an infant female chimpanzee born to this group began to explore the enclosure by herself, she tried to play with the chain that was connected to the stones. As the infant was still clumsy in her manual actions, the infant's hand or fingers could possibly have become tangled in the chain, causing damage. When the mother witnessed her infant playing with the chain, she approached her and smoothly removed the chain from the infant (Fig. 3). Similar behaviors were observed several times until the infant had matured. These examples indicate that the chimpanzee mother tried to stop a certain behavior of the infant, who benefited by being kept away from an unknown danger.

Premack (2007) stated that human teaching consists of three distinct actions involving observation, judgment, and modification. The teaching by inhibition performed by the chimpanzee mother illustrates her ability to observe and judge the situation experienced by the infant and appropriately modify its behavior.

Communication

Chimpanzee mothers and infants communicate using vocalizations and gestures. Hirata (2008) observed numerous interactions of mother–infant pairs in captivity. When infants were immature, mothers sometimes helped the infants to move. When the mothers traveled longer distances that might have been difficult for the infant to travel alone, the mother communicated with the infant, and they traveled together with the mother carrying the infant. For example, prior to travel, one mother stretched out her hand toward her offspring who was some distance away

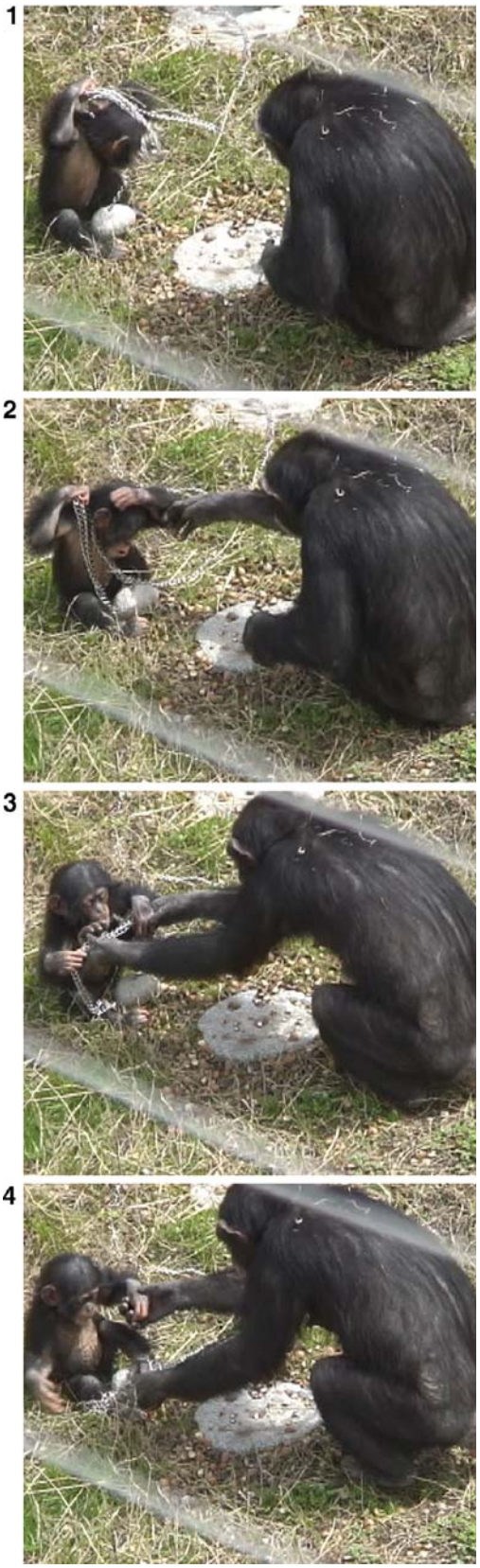

Fig. 3 A chimpanzee mother preventing her infant from rough play with chains

Fig. 4 A chimpanzee mother stretching out her hand to her infant

from her (Fig. 4). 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 one-third to one-half of cases, such contact between the mother and infant was established by mutual communication, and the longer the mother traveled, the more often she established contact with the infant to carry it. Hirata (2008) suggested that mothers may determine the goal of travel in advance and carry the infant if necessary, communicating with the infant in advance using several types of behaviors.

Several recent studies have focused on gestural communication in chimpanzees and have demonstrated that wild chimpanzees engage in referential communication (Pika and Mitani 2006). Pollick and de Waal (2007) demonstrated that the flexibility of gestural communication is greater compared to facial/vocal signals, which suggests that gestural communication may be the root of human language. The mother–infant relationship is the first social relationship that an infant experiences, and the ability to produce and understand gestural communication can be observed early in infancy. In this sense, the mother–infant relationship may have fostered the ability of gestural communication in primate evolution.

Concluding remarks

Advanced social intelligence in chimpanzees enables them to engage in deceptive interactions, perspective-taking, social learning, trading, and cooperative actions. Many studies have revealed that chimpanzees are proficient in using their social intelligence for selfish motives. In contrast, it is not yet clear whether these primates have tendencies to engage in prosocial behaviors to benefit others, and both positive and negative experimental evidences have recently been reported. However, episodes of chimpanzee mother–infant interactions indicate the possibility of prosocial behavior. Therefore, unlike the views of Premack (2007) and Vonk et al. (2008), I propose that chimpanzees possess rudimentary traits of human mental competence, not only in terms of theory of mind in a broader sense, but also in terms of prosociality involving regard for others.

De Waal (2008) argued that empathy plays a crucial role in altruistic behaviors. Three levels of empathy are postulated in his arguments: emotional contagion as the lowest level, sympathetic concern as the next evolutionary step, and empathic perspective-taking as the highest level. He describes the case of a mother ape who helps a whimpering juvenile move from one tree to the next as evidence of empathic perspective-taking, because the mother assesses the juvenile's goal and the specific reason for the youngster's distress. The case of mother chimpanzees communicating with their infants when they travel, as described in the earlier section, as well as the case of mother–infant food or object-sharing fit within the idea of empathic perspective-taking. A point of difference is that, in contrast to the example of a mother's helping her whimpering offspring in de Waal's (2008) paper, infant chimpanzees described in the above section do not show signs of distress. Therefore, in the first place, it is clear that the mothers' behaviors in the latter cases cannot be ascribed to emotional contagion or sympathetic concern. Rather, these cases indicate a possibility that chimpanzee mothers understand the situation of their infants and attempt to meet their needs even without emotional signals from the infants; this form of response may constitute a higher grade of empathetic perspective-taking.

Mother–infant relationships have experienced numerous changes during mammalian, primate, and hominoid evolution, from merely provisioning milk to long-term care by embracing (Matsuzawa 2006). Chimpanzee mother–infant interactions exhibit features common to humans, such as face-to-face communication (Tomonaga et al. 2004). The mother–infant relationship has become increasingly intense during the course of evolution and represents the relationship in which newborn infants first experience sociality. Therefore, it is quite logical to deduce that mother–infant interactions are key to understanding the manifestation of social intelligence from an evolutionary perspective.

Several studies have examined the cognitive ability of chimpanzee infants reared by humans, particularly in ape-language projects (e.g., Gardner and Gardner 1969). In addition, some research has investigated social intelligence between unrelated adults (e.g. Hirata and Matsuzawa 2001; Hirata and Fuwa 2007); however, little information is available regarding the sociocognitive abilities underlying

interactions between chimpanzee infants and their biological mothers (but see the "Ai project" since 2000; Matsuzawa 2003). Future studies are required to better understand both the continuities and discontinuities in cognitive traits between human and nonhuman animals and to reveal causes of the evolution of uniquely human cognitive faculties, such as complex, domain-general, and embedded understanding of the minds of others.

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