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How and When Do Chimpanzees Acquire the Ability to Imitate?

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1 Introduction

Imitation is an important activity in humans, since a large amount of communicative and adaptive learning is based on reproducing others' skills. Numerous psychologists have mainly emphasized two aspects of the function of bodily imitation. The first is social learning, which contributes to adaptive skills in the human environment. Within the second year of life, human infants acquire the ability to perform a wide variety of novel actions (e.g., tool-using behaviors, symbolic gestures) by imitation (Abravanel and Gingold 1985; Meltzoff 1988). Moreover, imitation is considered to play a key role in supporting human cultural traditions by assisting in the transmission of knowledge and skills from one generation to the next (Matsuzawa et al. 2001; Tomasello et al. 1993a).

The second aspect is communication. Several researches on human infants have suggested that imitation plays an important role in developing social cognitive abilities. For example, the ability to imitate others is considered to be *fundamental to the development of the normal theory of mind proposed by Premack and Woodruff (1978; Barresi and Moore 1996; Meltzoff and Gopnik 1993; Rogers and Pennington 1991)* as well as self-awareness and the awareness of others (Meltzoff 1990). Further, imitation is considered to be a precursor to the capacity to represent symbols such as language (Piaget 1962; Werner and Kaplan 1963).

The foregoing two aspects appear to suggest the significant evolutionary advantage of this critical ability. The question regarding the extent to which nonhuman species are capable of imitation has important implications for the biological and phylogenetic foundations of human cognitive complexity (Visalberghi and Frigaszy 1990; Tomasello et al. 1993b; Whiten and Custance 1996). In this chapter, I compare the imitative abilities of humans (*Homo sapiens*) and our closest evolutionary relatives—chimpanzees (*Pan troglodytes*)—to explore the unique aspect of human cognition from an evolutionary perspective. Moreover, I also discuss the imitative ability from a developmental per-

spective. In other words, I have focused on the development of imitation in chimpanzees, comparing it with the development of the same ability in humans.

2 Factors Influencing Imitation in Adult Chimpanzees

Thus far, most experimental studies have shown that chimpanzees do not imitate a broad range of actions to the same degree as humans (Custance et al. 1995; Hayes and Hayes 1952; Nagell et al. 1993; Tomasello et al. 1987; Whiten et al. 1996). If this is the case, what kinds of actions are difficult/easy for chimpanzees to imitate? Myowa-Yamakoshi and Matsuzawa (1999) systematically investigated the factors that determine the degree of difficulty faced by chimpanzees in imitating human actions in a face-to-face situation.

The subjects of the study were five female nursery-reared chimpanzees, from 12 to 19 years of age, belonging to the Kyoto University Primate Research Institute (PRI). They had participated in several cognitive experiments (Matsuzawa 2003). Four pairs of objects were used as test stimuli. Each pair consisted of two objects that differed from each other and had no explicit relationship. Each session consisted of three conditions: (a) one object (O), (b) one object to self (O to S), and (c) one object to another (O to O). In the O condition, the chimpanzees watched the demonstrator manipulate one object (e.g., hitting the bottom of a bowl). In the O to S condition, the demonstrator manipulated one object at certain positions on his body (e.g., placing a bowl on his head). In the O to O condition, the demonstrator manipulated one object with respect to another (e.g., hitting a ball with a bowl). These three conditions involved many different motor patterns (e.g., hitting, pulling, pushing).

The human demonstrator and the chimpanzee sat face to face during the sessions. Before the start of the test, a pair of objects was presented to the chimpanzee for approximately 3 min of free play. During this time, the chimpanzee interacted with each of the objects in some way. The demonstrator then retrieved the objects and began to demonstrate an action. Each action was demonstrated two or three times to ensure that the chimpanzee paid attention to the action. After an action was demonstrated, the chimpanzee was handed the objects and was told "Do this!" (Fig. 1).

We conducted the test in two phases, depending on the chimpanzee's responses. In the first phase, we observed the chimpanzee's responses during the first attempt to determine whether she could reproduce the demonstrated action (imitation phase). If the experimenters judged that the chimpanzee was able to perform the action, the next action was demonstrated. If the chimpanzee was unable to perform the demonstrated action, we proceeded to the teaching phase, in which the demonstrator trained the chimpanzee to perform the action using verbal guidance, gestures, molding, and shaping by rewarding the chimpanzee with verbal praise and food reinforcements. The demonstrator then repeated the model trial to show the action again and handed the objects to the chimpanzee. When the experimenters judged that the chimpanzee could

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Fig. 1. A chimpanzee (Chloe) performing the demonstrated actions in the one-object condition (rolling the hose)

perform the action three times in succession, we proceeded to the next action. The trial began with the initial response of the chimpanzee and ended either when the chimpanzee successfully performed the demonstrated action or after the demonstrator had taught the action. Any one action was repeated a maximum of 20 times.

The chimpanzee's responses were videotaped, and the motor patterns involved in the chimpanzee's responses in each trial were identified as 1 of 23 mutually exclusive types. These motor patterns were classified into two main categories: (a) general motor patterns that had been observed in the free play involving manipulation and (b) nongeneral motor patterns that were not observed in the free play. To assess the level of difficulty to reproduce an action, we counted the total number of trials that were required for each chimpanzee to successfully perform each demonstrated action and compared the mean number of trials across the three conditions and two categories of motor patterns.

As a result, we arrived at three important findings. First, the chimpanzees found it more difficult to perform actions involving novel motor patterns as compared to performing actions involving familiar motor patterns (Fig. 2). It was noteworthy that the chimpanzees seldom reproduced demonstrated actions in the first attempt, even when these actions involved motor patterns that they had already acquired. Second, the chimpanzees found it easiest to perform actions in the O to O condition. On the other hand, single-object manipulations were the most difficult to reproduce (Fig. 3). It seems likely that the chimpanzees focused on the direction in which objects were manipulated to acquire visual cues for reproducing the demonstrator's actions. Third, we found some very specific types of errors in the imitative task. The chimpanzees persistently repeated actions that they were taught in a previous session and also continued

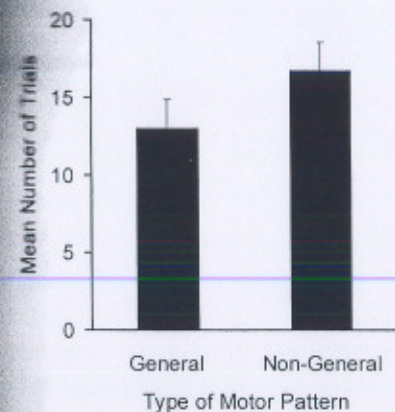


Fig. 2. Mean number of trials (plus standard error) required to perform the demonstrated actions in each of two conditions. *General*, motor patterns that were observed in the free play period; *Non-general*, motor patterns that were not observed during the free play period. [From Myowa-Yamakoshi and Matsuzawa (1999)]

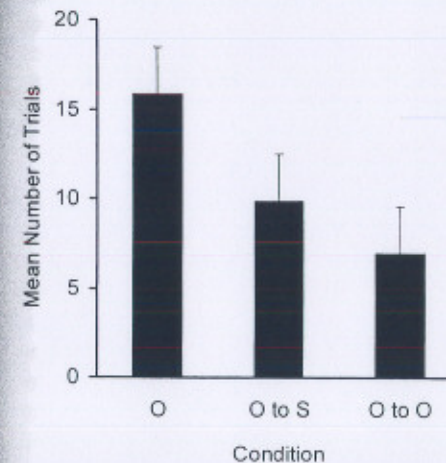


Fig. 3. Mean number of trials (plus standard error) required to perform the demonstrated actions in each of three conditions. *O*, the one-object condition; *O to S*, the one-object-to-self condition; *O to O*, the one-object-to-another condition. [From Myowa-Yamakoshi and Matsuzawa (1999)]

to manipulate each object in familiar ways. This finding indicates that their responses were somehow stimulus bound.

This study suggested that it is easier for chimpanzees to perform an action in which an object is directed toward some external location than to manipulate a single object alone. In addition, the chimpanzees were less likely to focus on the details of the demonstrator's body movements while manipulating an object; they paid more attention to the direction of the manipulated object. There were some constraints in the basic cognitive processes required to transform visual information into matching motor actions when the chimpanzees imitated human actions.

3 How Do Chimpanzees Represent Others' Actions?

It is possible that this basic difference in visual-motor information processing reflects the core differences between the social-cognitive abilities of humans and chimpanzees. The next question of importance was how the chimpanzees, with lower imitation skills, understood what the demonstrator did; in other words, how does the imitator represent the actions of others within a psychological framework (e.g., intention, desire) (Baron-Cohen 1995; Fodor 1983). Nonverbal tests have shown that human infants as young as 14 to 18 months old are capable of understanding something about the others' intentions (Carpenter et al. 1998; Meltzoff 1995). Meltzoff (1995) investigated the understanding of others' intentions in 18-month-old human infants. Meltzoff took advantage of the natural tendency of human infants to reproduce the actions of others, which is referred to as the "behavioral reenactment procedure." In this experiment, the infants saw that the demonstrator attempted but failed to reach the end state of an action (e.g., he attempted to pull on the ends of a dumbbell, but his hands slipped). After the demonstration, when given the opportunity to manipulate the object themselves, the infants could spontaneously achieve the end state of the actions as often as infants who saw the successful demonstration and more often than infants in the other control conditions. Meltzoff concluded that 18-month-old infants are capable of representing others' actions in a psychological framework—from body movements to the underlying goal or intention.

Experimental research on apes' understanding of others' actions has primarily focused on the differences between intentional and accidental actions, although these studies are few (Call and Tomasello 1998; Call et al. 2005; Povinelli 1991; Povinelli et al. 1998; Premack 1986). However, the results are mixed; they display both positive (Call and Tomasello 1998; Call et al. 2005; Povinelli 1991) and negative findings (Povinelli et al. 1998; Premack 1986).

We hypothesized that chimpanzees who have limited visual-motor information processing with regard to body movement should be capable of understanding that others' intentions differ from those of humans. Using the behavioral reenactment procedure (Meltzoff 1995), Myowa-Yamakoshi and Matsuzawa (2000) investigated whether chimpanzees are capable of understanding the demonstrator's intention and focused on the structure of the demonstrated actions to determine the types of cues that would be available for chimpanzees to understand others' intentions.

The subjects were five adult chimpanzees belonging to the PRI; they were the same five chimpanzees who were tested by Myowa-Yamakoshi and Matsuzawa (1999). A human demonstrator and a chimpanzee sat face to face. Eight pairs of objects were used as test stimuli. Each pair consisted of two objects. One was called the "container," and it required different patterns of motor operation to open (pushing, pulling, or twisting). The other was called the "irrelevant tool," and it was irrelevant to the opening of the container. Each session consisted of two phases of demonstration: (a) the demonstrator attempted but failed to open the container because one of his hands slipped off the container (failure phase)



Fig. 4. A chimpanzee (Chloe), sitting face to face with a human demonstrator, is performing the demonstrated action—trying to open a box with an irrelevant tool

and (b) the demonstrator successfully opened the container (success phase). Following the demonstrations in both phases, the chimpanzees were allowed to manipulate the objects by themselves. Each chimpanzee was introduced to the two phases in the order just mentioned. Moreover, in each phase—success and failure—the demonstrator manipulated the container using one of two alternative strategies: trying to open the container (a) using the irrelevant tool or (b) by hand (Fig. 4). We counterbalanced the chimpanzees to examine the alternative within each phase. The session consisted of a 3-min free play and the following two phases of imitation test (Fig. 5).

The results revealed that the chimpanzees were able to open the containers in the failure phase, although the cases were few (less than 11% of the total performances). Overall, no clear difference was observed between the performances in the failure and success phases with regard to actually opening the container. The chimpanzees did not appear to be more successful in opening the containers even after an actual demonstration was provided. However, they manipulated the objects using the demonstrated strategy significantly more often than other strategies (Fig. 6). These findings suggest that chimpanzees anticipate others' intentions mainly by perceiving the directionality and causality of object(s) as available cues. Recently, Call et al. (2005) also revealed similar results with chimpanzees using the procedure that Meltzoff (1995) used.

It appears that chimpanzees do not understand others' intentions in the same way that humans do. Human infants understand others' intentions in a psychological framework through body movement. On the other hand, in the case of chimpanzees, the anticipation of others' forthcoming actions by perceiving the directionality and physical causality of objects is a more available cue than others' body movements performing the manipulation. Thus, compared to the

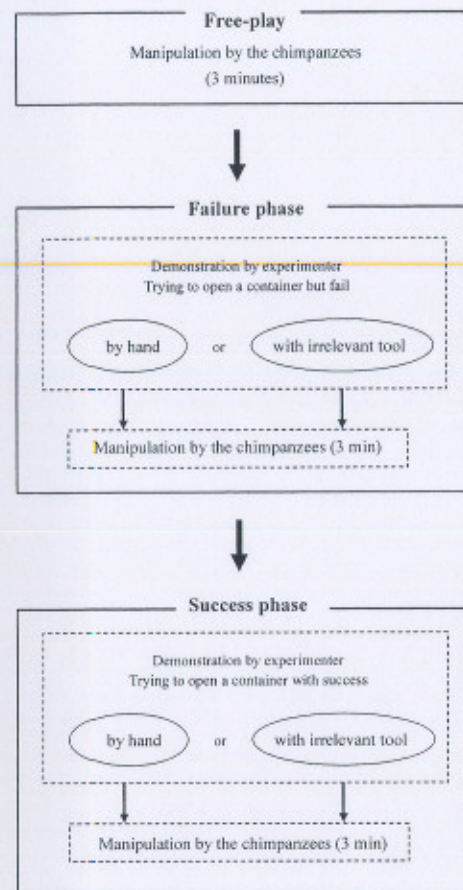


Fig. 5. Experimental procedure. [From Myowa-Yamakoshi and Matsuzawa (2000)]

current task, we may speculate that chimpanzees could find it more difficult to distinguish actions having the same outcomes or body movements to understand others' intentions.

4 Development of Imitation Abilities in Human Infants

Let us now consider the imitative abilities of human infants from a developmental perspective. The most comprehensive theory on the development of imitation is that by Piaget (1962). Piaget postulated six stages of action imitation by infants, which may be divided into three main levels. In the first level (from birth to 8 months), human imitation is restricted to imitating simple hand opening.

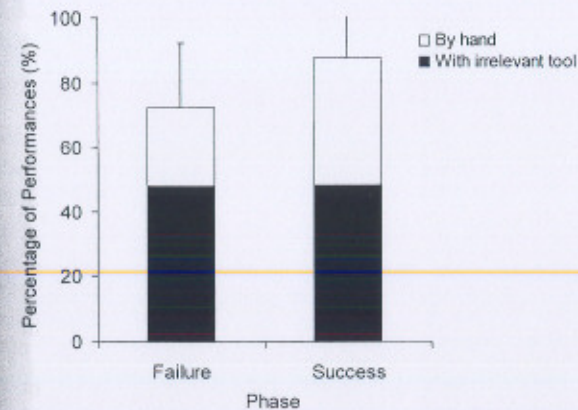


Fig. 6. Percentage of performances (plus standard error) by the chimpanzees using the identical strategies shown by the demonstrator in both the phases. [From Myowa-Yamakoshi and Matsuzawa (2000)]

This type of imitation can be accomplished through an intermodal matching process. Human infants can directly compare the demonstrator's hand movements with those of their own visible hand. In the second level (from 8 to 12 months), human infants begin to imitate facial gestures without intramodal guidance. Infants cannot see their own facial gestures, such as opening their mouths. Facial imitation depends on a cross-modal matching process. The important development in the third level is deferred imitation, and it appears at approximately 18 months. Deferred imitation is not performed during the demonstration. Piaget postulated that deferred imitation involves the infants' representational capacities and is a precursor to representing symbols such as language.

In contrast to Piaget's hypothetical framework, Meltzoff and Moore (1977) experimentally showed that human neonates can imitate some of the facial gestures [tongue protrusion (TP), lip protrusion (LP), and mouth opening (MO)] of the demonstrators. Numerous studies have been conducted on neonatal imitation including the imitation of other facial expressions (Abravanel and Sigafoos 1984; Heimann 1989; Field et al. 1982), such as eye blinking, head and finger movements, and cheek movements (Fontaine 1984; Meltzoff and Moore 1992, 1994; Reissland 1988; Vinter 1986). Meltzoff and Moore (1977, 1983) speculated that human infants can imitate motor acts performed by others through active intermodal matching (AIM), which is mediated by an innate representational system. According to the AIM hypothesis, human neonates can directly map the visible motor movements of others through their own nonvisible but felt movements.

5 The Origin of Imitative Ability: Does Imitative Ability Arise from Neonatal Imitation?

Several alternative views have been proposed on how neonatal imitation can be interpreted. For example, some researchers have insisted that this type of neonatal imitation is mediated by an "innate releasing mechanism" based on simple reflexes such as the Moro reflexion (Abravanel and Sigafos 1984; Jacobson 1979). A powerful argument supporting this view is that neonatal imitation either disappears or declines at approximately 2 to 3 months of age and reappears later (Abravanel and Sigafos 1984; Fontaine 1984; Maratos 1982). These data are assimilated into the reflexive view by proposing that the initial drop in imitation corresponds with the inhibition of other reflexive responses.

However, Meltzoff and Moore (1992) insisted that facial imitation does not necessarily disappear at 2 to 3 months of age. They emphasized that neonatal imitation facilitates social communication, that is, it helps infants to understand the concept of "people" as opposed to "things" and aids their identification of specific people. Infants may use imitation to verify identities when engaging in face-to-face social interactions with adults. In addition, Meltzoff and Moore argued that, contrary to the reflexive view, the apparent disappearance of imitative responses observed in 2- to 3-month-olds is actually because older infants respond to people by engaging in social interaction games more frequently than neonates.

It remains unclear whether we should interpret neonatal imitation as imitative behavior. However, both these views are very similar with respect to the role of neonatal imitation. Researchers espousing these views emphasize that neonatal imitation may serve a social communicative function. Neonatal imitation may play a crucial role in attracting the attention of adults and increasing interaction opportunities for receiving care.

6 How Do Chimpanzees Acquire the Ability to Imitate?

Little is known about the existence and development of neonatal imitation in nonhuman primates (Bard and Russell 1999; Myowa 1996). It was only in 2000 that we were able to systematically investigate the imitation of facial expressions in chimpanzees immediately after birth by following a testing procedure identical to that used for human neonates (Meltzoff and Moore 1977; Myowa-Yamakoshi et al. 2004).

The subjects, two neonatal chimpanzees named Ayumu and Pal, were both born after a complete gestation period. They were reared by their biological mothers, who had participated in several cognitive experiments in PRI. They had also participated in a variety of tests related to the development of cognitive abilities (Matsuzawa 2003; Tomonaga et al. 2004).

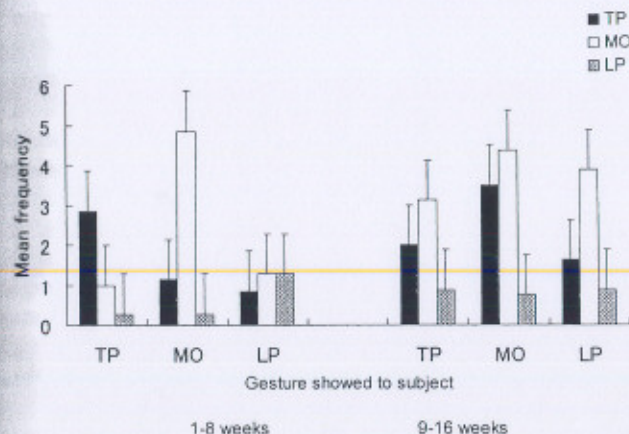


Fig. 7. The frequency of the three gestures (tongue protrusion, mouth opening, and lip protrusion) during 1 to 8 and 9 to 16 weeks of age (plus standard error). The x-axis plots the facial gestures shown to each chimpanzee for each period. TP, tongue protrusion; MO, mouth opening; LP, lip protrusion (Ayumu). [From Myowa-Yamakoshi et al. (2004)]

The test was conducted once a week for chimpanzees that were 1 to 16 weeks of age. A human tester and the chimpanzee, held by its mother, sat face to face. Before the experiment began, the tester presented the chimpanzee with an unresponsive passive face (lips closed, neutral facial expression). To sustain alertness and ensure the neonate's visual fixation on the tester's face, auditory stimulation (calling out the neonate's name once or twice) was provided before each trial. The neonate was then shown one of the following three gestures in a random order: TP, MO, or LP. In each trial, the tester demonstrated each gesture four times over a 15-s stimulus-presentation period. A 20-s response period followed immediately after. In the response period, the tester stopped making the facial gestures and displayed a passive face.

Figure 7 presents the mean frequency of each of the three gestures (TP, MO, and LP) performed by Ayumu over the two periods. These results show that at 1 to 8 weeks of age both infants were successful in producing a greater number of TP and MO responses when the TP and MO were demonstrated. However, their imitative responses of TP and MO disappeared after 9 weeks of age. Figure 8 shows the imitative responses of the three demonstrated facial gestures by Pal.

Taking these facts into consideration, we provided positive evidence for neonatal imitation in chimpanzees. At less than 7 days of age, the chimpanzees could discriminate between and imitate several human facial gestures. However, by the time they were 2 months old, the chimpanzees no longer imitated the gestures. They began to perform the MO gesture frequently in response to any of the three facial gestures presented to them. This response could be considered as "social

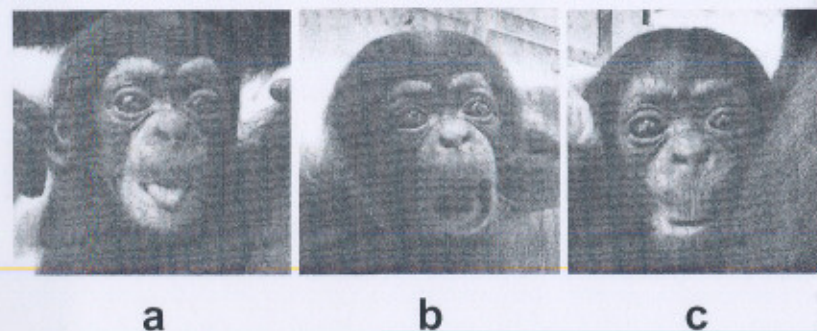


Fig. 8. Imitative responses of the three demonstrated facial gestures, tongue protrusion (a), mouth opening (b), and lip protrusion (c), by Pal at 2 weeks of age. [From Myowa-Yamakoshi et al. (2004)]

smiling" (i.e., play face) directed at the human experimenter. Although the reason for the disappearance of facial imitation in chimpanzees is still unknown, it is possible that the social-interactive responses toward the experimenter might have influenced the disappearance (Metzoff and Moore 1992).

We also conducted experiments on neonatal imitation by squirrel monkeys, Japanese monkeys, and a lesser ape, a gibbon, from the time of their births. However, no clear evidence of neonatal imitation was observed (Fig. 9) (Tomonaga et al. 2003). These results suggest that they might not have the same early imitative abilities as humans and chimpanzees.

To reveal whether facial and bodily imitation in chimpanzees reappears with age, we continued to examine the imitative ability of the two chimpanzees over a period of 3 years. It was interesting to note that at around 9 months the chimpanzee infants again began to produce imitation-like responses for several facial gestures. They differentially produced the three demonstrated actions—TP, MO, and LP. In addition to the facial gestures, they also produced imitation-like responses in the form of simple bodily movements such as hitting. We may refer to their responses as "imitation-like" because their imitative responses were somewhat different from human imitation. That is, the chimpanzees' reproduction of the observed actions was always accompanied by body contact with the experimenter (Fig. 10) (Myowa-Yamakoshi 2004).

7 Body Mapping or Teleological Stance?

As suggested earlier, adult chimpanzees appear to be less sensitive to body movements than to the manipulated objects involved in the demonstrated actions. Our findings are consistent with several experimental studies of observational learning in chimpanzees. For example, Tomasello et al. (1987) and Nagell et al. (1993) investigated observational learning on tool-using behaviors in humans

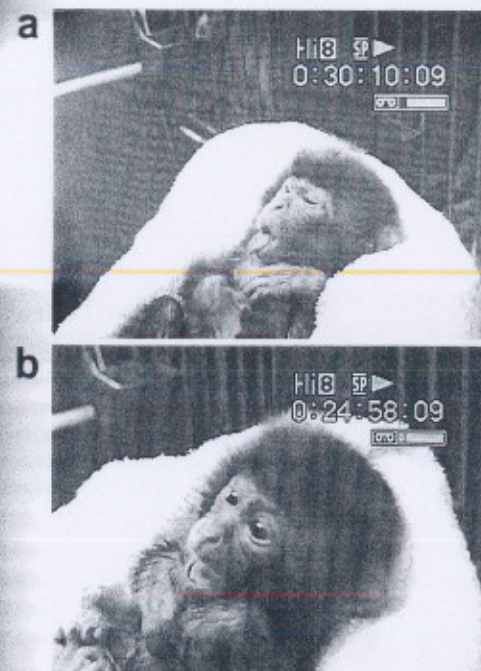


Fig. 9. Facial responses for the demonstrated facial gestures in a Japanese monkey: tongue protrusion (a) and mouth opening (b)

and captive chimpanzees. They suggested that although the human children faithfully copied the demonstrated methods of tool use, the chimpanzees did not pay attention to the precise methods involved in accomplishing the task: they tried to achieve only the results by performing the motor actions that were already in their repertoire in a trial-and-error manner. To distinguish this type of observational learning from human-specific imitative learning, Tomasello and his colleagues (Tomasello et al. 1993b; Tomasello 1999) have termed it as learning as "emulation."

Again, let us consider the imitation-like responses that the infant chimpanzees produced around 9 to 10 months of age. Did they reproduce the observed actions in a chimpanzee-specific manner, that is, emulation? In what way were their imitative outputs constructed from perceived actions performed by the model? Theoretical models proposed by recent human cognitive developmental researches appear to be useful in exploring these questions.

According to the AIM mechanism by Metzoff and Moore, humans have an innate ability to automatically match motor programs by direct perceptual-motor mapping. This mechanism is considered to enable humans to imitate bodily gestures immediately after birth. The direct mapping view of imitative behaviors has been supported by recent neurophysiological discoveries such as mirror neurons (Fadiga et al. 1995; Rizzolatti et al. 1996).

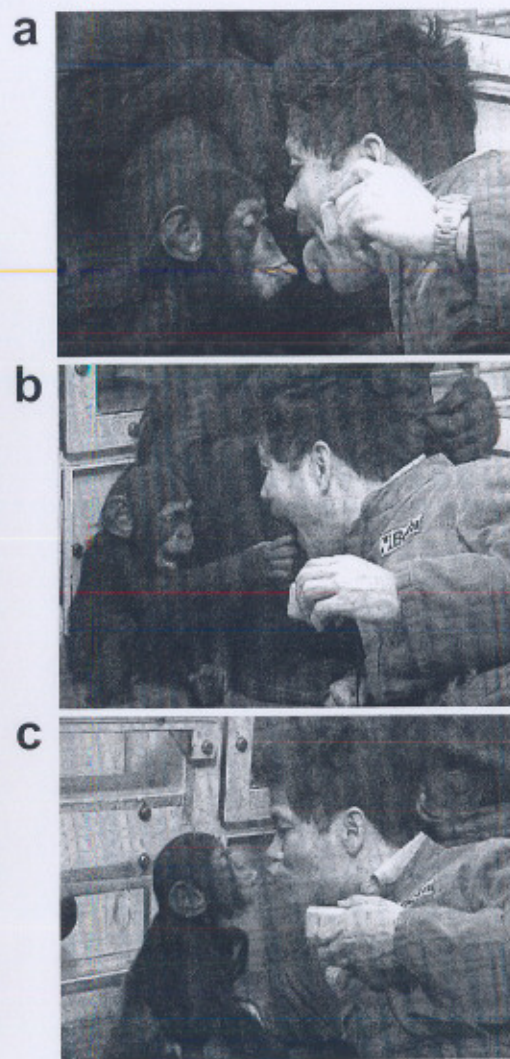


Fig. 10. Imitative responses of the three demonstrated facial gestures, tongue protrusion (a), mouth opening (b), and lip protrusion (c), by Ayumu at 9 months of age. [From Myowa-Yamakoshi (2004)]

However, recent empirical evidence indicates another view—the development of imitation may be mediated by extracting the represented goals, rather than matching constituent kinematic primitives in the observed actions. For example, Bekkering et al. (2000) investigated the imitation of goal-directed actions in children 3 to 6 years of age. The demonstrated goal-directed actions consisted of touching either their right or their left ear with either an ipsilateral or a contralateral hand movement. When the contralateral hand movements were

demonstrated (e.g., the demonstrator touched his left ear with his right hand reaching across his body), the children often touched their corresponding ear with an ipsilateral rather than a contralateral hand movement. Bekkering et al. insisted that the young children did not necessarily and automatically copy the demonstrated actions. In conclusion, they proposed that children may begin to learn how to build the necessary motor structures based on a goal-directed perspective instead of an active matching-to-target perspective, as postulated in the AIM mechanism. Similarly, Gergely et al. (2002) suggested that human infants modulate their imitative behavior according to the justifiability of the goal-directed actions performed by the demonstrator. They demonstrated that if the action could be rationalized by the situational constraints of the model, and if the situational constraints of the infant differed, it would prevent 14-month-olds from imitating the observed actions. Rather, they attempted to achieve the same goal by the most rational action available within their own situational constraints. Gergely and Csibra (2003) proposed that even 1-year-olds can interpret others' actions as goal directed to represent observed actions. They have termed this teleological interpretational system as the “teleological stance.” Moreover, they mentioned the possibility that this early teleological stance is associated with the ability to attribute mental states to others (i.e., beliefs, desires, and intentions), an ability that would emerge only later.

We demonstrated that chimpanzee neonates also displayed the ability to imitate several facial gestures. This evidence suggests the possibility that humans and chimpanzees share the innate AIM mechanism. The phenomenon of neonatal imitation found in both the species could be mediated by a direct mapping process, based on a supramodal representational system that matches the perceptual information of the observed act with the proprioceptive information of the produced act. On the other hand, the imitation-like behaviors of older chimpanzees do not appear to be captured by the direct perceptual-motor mapping view. In contrast to human infants, the young chimpanzees only rarely match the visually perceived and motor outputs in the absence of bodily contact with the demonstrator.

Let us consider their imitation-like responses on the basis of another view—the teleological stance. It is possible that the chimpanzees can interpret the demonstrated actions by extracting their goal states. For example, they might interpret the demonstrated facial gestures, such as kissing and smiling, as the communicative signals directed toward them. It is possible that they interpret the demonstrated action ‘hitting’ as an invitation to a social game. Unfortunately, we were able to demonstrate only simple arbitrary bodily movements in young chimpanzees. These actions did not have the obvious nature of goals as in the case of manipulations of functional objects. Therefore, it would have been difficult to discuss their imitation-like responses by distinguishing the two views, active matching-to-target and active matching-to-goal perspectives.

It is still unclear whether and how young chimpanzees can construct motor output based on their perception of actions performed by a demonstrator. Further research is required to investigate the way in which chimpanzees develop

their imitative abilities based on direct perceptual-motor mapping or teleological stance. This point is important to reveal how early imitation in chimpanzees is developmentally linked not with human-specific imitation but with a chimpanzee-specific observational learning ability, namely, emulation. Further, if the teleological stance is present in young chimpanzees, we might discuss whether or not this early ability is related to the later emergence of the mentalistic stance from an evolutionary perspective (theory of mind; Premack and Woodruff 1978).

8 Others as a “Mirror”

Finally, I must point out an external essential factor in the development of imitation, particularly in the case of humans. In the day-to-day interaction between human caregivers and infants, we notice social turn-taking behaviors that are considered to play an important role in the development of imitation. For example, caregivers pay a considerable amount of attention to infants' behaviors and react to infants' responses promptly. They introduce the infants to several facial expressions in the “exaggerated” mode, such as raising their eyebrows, opening their mouths wider, and smiling to attract the complete attention of the infants. In addition, they often imitate the responses of the infants. Similarly, infants are attracted to the caregivers' changeable and attractive gestures and respond to them. Such social imitative turn-taking games might increasingly reinforce infants' imitative abilities. It is probable that through turn-taking games with caretakers, human infants might begin to interpret others' actions as intentional or goal directed (teleological stance) by the end of the first year (Gergely and Csibra 2003).

Mothers and infants among both wild and captive chimpanzees also engage in face-to-face interactions (Fig. 11). Bard et al. (2005) investigated the number of mutual gazes between mother and infant chimpanzees belonging to PRI during the first 3 months. When the infants reached 6 to 8 weeks of age, the frequencies reached a peak; the number of mutual gazes was 27 per hour. However, it is reasonable to say that the frequency of mutual gazes in chimpanzees was not as high as that observed in humans. Moreover, in the species-typical environment, both in the wild and in captivity, not much research has been conducted on the imitative games between mother and infant chimpanzees, in contrast to humans.

Interestingly, Tomasello et al. (1993b) suggest that the chimpanzees reared in a human-like social environment (enculturated) might develop a more imitative ability than the mother-reared chimpanzees. It is possible that the imitative ability develops flexibly, depending on extended exposure to the surrounding rearing environments after birth. Is it possible that infant chimpanzees reared by enculturated chimpanzees can develop higher imitative abilities? Are there any differences in the representation that mediates the perceptions and actions in imitation between the enculturated and mother-reared chimpanzees? Is it possible that the enculturated monkeys would also develop imitative abilities? Further longitudinal developmental and comparative studies will help in reveal-



Fig. 11. Mutual gazing between a mother (Chloe) and her infant (Cleo, 1 year 11 months). (Photo by Tomomi Ochiai)

ing the relationship between species-specific biological foundations and the effect of the postnatal social experience in the development of imitation.

9 Conclusion

Our findings suggest a discontinuity between neonatal imitation and imitation that develops later in life. The capacity for neonatal imitation could be a characteristic that is common to humans and chimpanzees and has resulted from natural selection. On the other hand, the ability to imitate a broad range of whole-body actions, particularly those that do not involve objects (e.g., sign language, pantomime), appears to be an ability that is unique to humans. There may be some constraints in the cognitive processes required to transform visual information into matching motor acts in chimpanzee imitation. It is possible that this basic difference in visual-motor information processing reflects the differences in the early ability to interpret others' actions as being intentional and goal directed; it also reflects the difference in the ability to attribute mental states to others, such as beliefs, desires, and intentions in both chimpanzees and humans. It can thus be said that the later imitation might have evolved after the human lineage separated from that of chimpanzees (Myowa-Yamakoshi 2001). This more complex imitative ability in humans might have played a key role in producing unique human cultures.

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15 Yawning: An Opening into Empathy?

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1 On Empathy in Great Apes

Comparative developmental psychologists are interested in the emergence and development of empathy in both humans and nonhumans. By empathy, we mean the ability to identify with another individual's emotions and cognitive states; it is characteristic of all normal humans from early childhood. Even today there is debate among primatologists and psychologists about whether and to what extent our nearest evolutionary neighbors, the great apes, share the capacity for empathy that we humans take for granted (Gallup 1998; Preston and de Waal 2002; Povinelli 1998; Povinelli and Vonk 2003; Tomasello et al. 2003). Although many people who work closely with these primates are convinced that they are capable of reflecting about what other individuals might be thinking, others express doubts about the extent and level at which they do this. Much of the controversy stems from the variable quality of the evidence presented in support of empathic abilities. The evidence comes from a range of observational studies and controlled experiments, and as we will see from our brief review of the literature as it concerns chimpanzees, neither source of data is problem free.

Observational studies of chimpanzees in the wild and in naturalistic groups in captivity have led to identification of a range of phenomena suggestive of the capacity for empathy in these apes (O'Connell 1995). For example, some advanced forms of deception may involve attributing intentions to other individuals and deliberately altering others' beliefs, emotions, or attentional states. The evidence for intentional deception of this type is stronger for chimpanzees than for any other species of nonhuman primates (Byrne 1995; Byrne and Whiten 1992). One of the best known examples took place in a captive group with access to a large outdoor enclosure. Menzel (1974) described how one chimpanzee, Belle, would try to feign disinterest or misdirect another chimpanzee, Rock, away from some hidden food of which only she knew the location. Rock in turn began to feign disinterest in Belle's activities, only to suddenly wheel round to detect unintentional cues from Belle about where the food might be.

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