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REPORT

Imitation in neonatal chimpanzees (*Pan troglodytes*)

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Abstract

*This paper provides evidence for imitative abilities in neonatal chimpanzees (*Pan troglodytes*), our closest relatives. Two chimpanzees were reared from birth by their biological mothers. At less than 7 days of age the chimpanzees could discriminate between, and imitate, human facial gestures (tongue protrusion and mouth opening). By the time they were 2 months old, however, the chimpanzees no longer imitated the gestures. They began to perform mouth opening frequently in response to any of the three facial gestures presented to them. These findings suggest that neonatal facial imitation is most likely an innate ability, developed through natural selection in humans and in chimpanzees. The relationship between the disappearance of neonatal imitation and the development of social communicative behavior is discussed from an evolutionary perspective.*

Introduction

Humans have created and use a vast assortment of tools, and have also developed an extensive array of ways to communicate with each other. Imitation plays a key role in supporting human cultural traditions by facilitating the transmission of knowledge and skills from one generation to another (Tomasello, Kruger & Ratner, 1993; Matsuzawa, Biro, Humle, Inoue-Nakamura, Tonooka & Yamakoshi, 2001).

Within their first year of life, humans begin to imitate a range of novel and arbitrary acts (Piaget, 1962; Meltzoff & Moore, 1977, 1983). Human neonates 12 to 21 days of age can imitate human facial gestures (tongue protrusion, mouth opening and lip protrusion) without visual feedback of their own behavior (Meltzoff & Moore, 1977). This neonatal imitation is probably accomplished through active inter-modal matching (AIM), mediated by an innate representational system (Meltzoff & Moore, 1977, 1983, 1997). According to the AIM hypothesis, human neonates can cross-modally process visual and motor information and detect the equivalent motor response. Subsequent imitative ability is then thought to arise from this neonatal behavior.

An alternative explanation for neonatal imitation has, however, been proposed. This view holds that neonatal imitation is mediated by an 'innate releasing mechanism', based on simple reflexes such as the Moro reflex (Jacobson, 1979; Abravanel & Sigafoos, 1984). Anisfeld (1996) insisted that tongue protrusion is the only gesture that clearly produces matching behavior and suggested that it is a specific, directly elicited response, and not the result of a cross-modal matching process. An argument for this second view is that neonatal imitation disappears or declines at approximately 2 to 3 months of age, and later reappears (e.g. Maratos, 1982; Abravanel & Sigafoos, 1984; Fontaine, 1984). These data are explained by the reflexive viewpoint, which sees initial imitation fading as other reflexive responses are inhibited.

On the other hand, Meltzoff and Moore (1992) proposed that neonatal imitation does not necessarily disappear at 2 to 3 months of age. The apparent disappearance of imitative responses in 2- to 3-month-olds may be because older infants respond to people by engaging in social interaction games (e.g. smiling and cooing) more vigorously than do neonates. Such social games are thought to mask imitation by older infants and the underlying competence at facial imitation.

It remains unclear whether cross-modal matching underlines neonatal imitation. Chimpanzees (*Pan troglodytes*), our closest evolutionary relatives, have much in common with humans, especially during the early developmental stages. Some studies have indicated that human and chimpanzee neonates perform similarly on the same

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tests (Mathieu & Bergeron, 1981; Hallock, Worobey & Self, 1989; Bard, Platzman, Lester & Suomi, 1992). For example, Bard *et al.* (1992) suggested that neonatal chimpanzees are capable of sustained attention to visual stimuli, as measured by the Brazelton Neonatal Behavioral Assessment Scale (NBAS). In addition, from birth throughout the neonatal period (30 days), chimpanzees respond significantly more often to social stimuli (e.g. a human face) than to nonsocial stimuli (e.g. a red ball).

Little is known about the existence and development of neonatal imitation in nonhuman primates (Myowa, 1996; Bard & Russell, 1999; Bard, submitted). Myowa (1996) showed that at 5 to 10 weeks of age a single infant chimpanzee could imitate tongue protrusion and mouth opening. However, as this experiment used a 5-week-old subject, raised by humans shortly after its birth, it is possible that its capacity for facial imitation was the result of postnatal human-type socializing. Recent data suggest that juvenile and adult chimpanzees imitate to the extent that they have had prior experience with human interaction (Tomasello, Savage-Rumbaugh & Kruger, 1993; Tomasello & Call, 1997; Myowa-Yamakoshi & Matsuzawa, 1999, 2000). The Myowa (1996) study needs to be replicated before its findings can help to explain the origins of imitation in nonhuman primates.

The purpose of our study was to test the imitation of human facial expressions in chimpanzee neonates during the immediate post-birth period, following a testing procedure identical to that used for human neonates (Meltzoff & Moore, 1977). As the neonates in this study were reared by their biological mothers, the effects of their early experiences with humans were assumed to be negligible. The study was designed to determine which characteristics of innate neonatal imitation are shared by humans and chimpanzees, regardless of postnatal experience.

Another purpose of this study was to assess the longitudinal development of facial imitation. We investigated imitative behavior through the first 16 weeks of life to determine whether imitative responses would change over time. Comparing the responses of the chimpanzee subjects with those of humans, we explored the foundations of imitation and we discuss its adaptive significance from both evolutionary and developmental perspectives.

Methods

Subjects

We studied two neonatal chimpanzees, a male named Ayumu and a female named Pal. Both infants were sired by the same father, conceived through artificial insemination, and born at full term (235 days). Their mothers had participated in several previous cognitive experiments (Matsuzawa, 1985; Tanaka, 1996; Myowa-Yamakoshi & Matsuzawa, 1999, 2000; Kawai & Matsuzawa, 2000; Tomonaga & Matsuzawa, 2002).

Procedure

We invited the mother–infant pair to an experimental booth; then a human experimenter sat face-to-face with the subject, which was held by its mother. To assess developmental changes in neonatal imitation, the chimpanzees were tested once a week, from 1 to 16 weeks of age (except for Ayumu at 6 weeks, and Pal at 7 weeks). The experimental procedure was almost identical to that of Meltzoff and Moore (1977). Two different adults served as experimenters for both subjects. The experimenter held a small CCD camera and recorded the subjects' facial responses using the camera (Sony, CCD-MC100; see Figure 1). Before the experiment began, the experimenter presented a non-reactive 'passive face' (lips closed, neutral facial expression) to the subject. Auditory stimulation (calling the neonate's name once or twice) was used before each trial to sustain alertness and to encourage the neonate to fixate visually on the experimenter's face. When a neonate spontaneously looked at the face, the neonate was then shown the following three facial gestures in random order: tongue protrusion, mouth opening and lip protrusion.

Within each session, the experimenter demonstrated each gesture four times during a 15-second stimulus presentation period, which was followed immediately by a 20-second response period. During the response period, the experimenter displayed a passive face. The stimulus presentation periods and the corresponding response periods were repeated up to two times for any one gesture if the neonate did not attend to the experimenter's presentation or his/her mother moved around the booth within 3 seconds of the experimenter presenting a stimulus. During the test periods, the infant chimpanzees never looked at their mothers' faces. This test was conducted on 2 days each week.

Scoring and behavioral definitions

Regarding the methodology, we did not analyze the data in the same way as Meltzoff and Moore (1977) because their first study has been regarded as controversial. Instead, we counted the frequencies of tongue protrusion, mouth opening and lip protrusion as dependent variables, according to the modified version of Meltzoff and Moore (1992). Videotapes were coded for each infant in all experimental sessions. The videotapes

Figure 1 *One of the two subjects, Ayumu, held by his mother, named Ai, while facing a human tester, performs the previously demonstrated action (mouth opening) (Photo by Nancy Enslin, Produced by Yomiuri Shinbun).*

consisted solely of close-up images of the subject's face. Recordings of the stimulus presentation were omitted.

Scoring criteria for the two oral behavioral responses, tongue protrusion and mouth opening, were adopted from Meltzoff and Moore (1983). Tongue protrusions (TPs) were defined as forward movements of the tongue such that it crossed the inner edge of the lower lip. In cases when the tongue was being retracted, but was not yet behind the lip when a second tongue thrust occurred, we scored these responses as one tongue protrusion. A mouth opening (MO) was scored when a visible downward movement of the lower jaw parted the infant's lips. Two successive downward jaw movements were scored as two MOs if separated by an upward jaw movement, otherwise the movement was identified as one continuous MO. Lip protrusions (LPs) were defined as forward movements of the lips when the tongue did not cross, and was behind the lips. Any other infant behaviors that occurred, such as yawning, sneezing, choking and swallowing, were not scored.

The recordings of the response periods of 90 trials (3 gestures × 15 weeks × 2 subjects) were counted by two coders. From slow-motion viewing of the videotapes, the raters were instructed to count the frequencies of the three gestures within each response. To insure the reliability of the data, one judge checked all trials, while the other judge, who was blind both to the purpose of the study and to which gesture the infant was shown, scored 13.3% of the total videotaped responses for each infant. Reliability between the two judges was sufficiently high (Cohen's kappa, Ayumu; 0.73, Pal; 0.81).

Myowa (1996) suggested that chimpanzees' neonatal imitative behavior disappears at around 10 weeks of age. In order to investigate changes in neonate responses over time, we analyzed the data in two periods: (1) 1 to 8 weeks after birth, and (2) 9 to 16 weeks after birth. Visual fixation on the experimenter during the stimulus presentation did not differ significantly among facial expressions [$F_{(2,28)} = 0.15$, $p = .85$ (Ayumu); $F_{(2,28)} = 0.27$, $p = .67$ (Pal); two-tailed], or between the two periods [$p = .45$ (1–8 weeks); $p = .28$ (9–16 weeks), paired test, two-tailed]. The mean (± SD) fixation times in seconds were as follows: Ayumu, 12.50 ± 2.46 (1–8 weeks), 13.06 ± 1.72 (9–16 weeks); Pal, 10.21 ± 2.35 (1–8 weeks), 12.31 ± 2.02 (9–16 weeks); Ayumu, TP, 12.82 ± 1.61, MO, 12.79 ± 2.19, LP, 13.14 ± 1.89; Pal, TP, 11.64 ± 1.95, MO, 12.07 ± 2.40, LP, 11.54 ± 2.72.

Results

Figures 2a and 2b present the mean frequency of each of the three gestures (TP, MO and LP) that each subject performed in the two periods. The *x*-axis plots the facial gestures that the model showed to each subject for each period. For the data on Ayumu for 1–8 weeks of age, the Friedman nonparametric repeated measure test showed significant differences between the frequencies of the three gestures in the TP demonstration ($Fr = 13.00$, $p < .01$) and MO demonstration ($Fr = 11.14$, $p < .01$). For the TP demonstration, post-hoc multiple comparisons using Wilcoxon tests with Ryan's correction procedure revealed a significant difference between TP versus LP ($p < .05$)

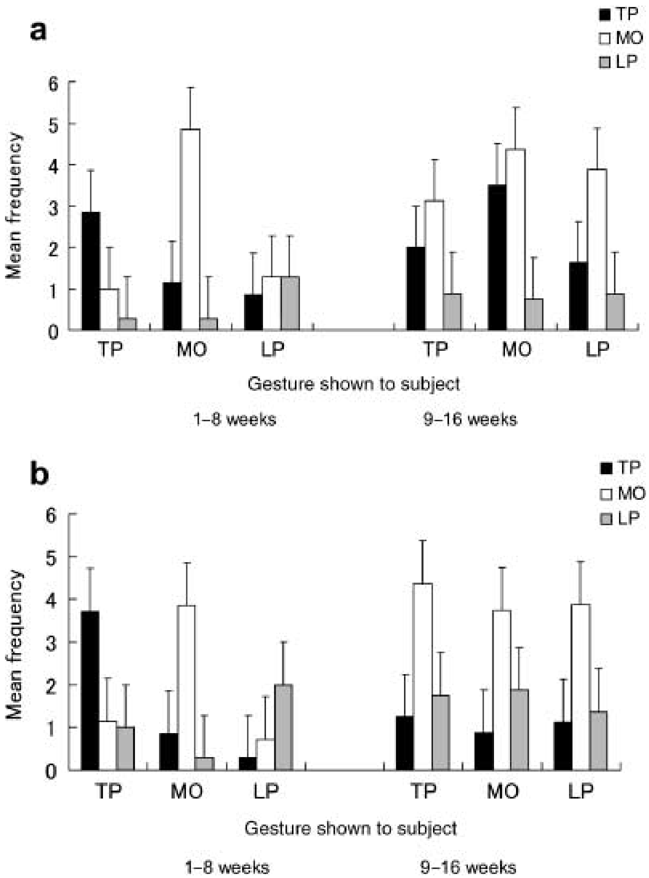

Figure 2 *The frequency of the three gestures (tongue protrusion, mouth opening and lip protrusion) in the periods 1 to 8 weeks and 9 to 16 weeks of age (plus standard error). (a) Ayumu, (b) Pal. The* x*-axis plots the facial gestures that the model showed to each subject for each period. TP = tongue protrusion, MO = mouth opening, and LP = lip protrusion.*

and a significant trend between TP versus MO ($p < .10$). For the MO demonstration, a significant difference was found between MO versus LP ($p < .05$) and a significant trend between MO versus TP ($p < .10$). Regarding the data for Pal at 1–8 weeks of age, the Friedman nonparametric repeated measure test showed significant differences between the frequencies of the three gestures in all three demonstrations (TP; $Fr = 10.32$, $p < .01$, MO; $Fr = 11.14$, $p < .01$, LP; $Fr = 8.2$, $p < .05$). For TP, Wilcoxon tests revealed a significant difference for TP versus LP ($p < .05$) and a significant trend between TP versus MO ($p < .10$). For MO, a significant difference was found for MO versus LP ($p < .05$) and a significant trend between MO versus TP ($p < .10$).

For the data for Ayumu at 9–16 weeks of age, the Friedman nonparametric repeated measure test showed significant differences between the frequencies of the three gestures in the TP demonstration ($Fr = 11.62$, $p < .01$) and MO demonstration ($Fr = 11.67$, $p < .01$). For the TP

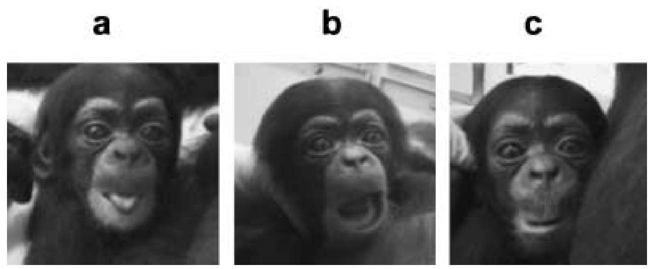

Figure 3 *The imitative responses of the three demonstrated facial gestures. (a) Tongue protrusion, (b) Mouth opening and (c) Lip protrusion (Pal, 2 weeks of age).*

demonstration, Wilcoxon tests revealed a significant difference for MO versus LP ($p < .05$). For MO, a significant difference was found for MO versus LP ($p < .05$). For the data for Pal at 9–16 weeks of age, the Friedman nonparametric repeated measure test showed significant differences between the frequencies of the three gestures in the TP demonstration ($Fr = 8.54$, $p < .05$) and MO demonstration ($Fr = 6.67$, $p < .05$). For the TP demonstration, Wilcoxon tests revealed a significant difference for TP versus MO ($p < .05$). For MO, a significant trend was found for TP versus MO ($p < .10$).

These results demonstrate that at 1–8 weeks of age, both infants were successful in producing more TP and MO responses when TP and MO were demonstrated, respectively. However, their imitative responses of TP and MO disappeared after 9 weeks of age.

Discussion

This study clearly demonstrated that chimpanzee neonates younger than 1 week of age are able to imitate human gestures of tongue protrusion and mouth opening (Figure 3). Our results revealed that facial imitation in the neonatal period in chimpanzees is not limited to tongue protrusion alone. Since the subjects were so young, it is unlikely that learning could account for their imitative abilities. The data suggest that, like human neonates, chimpanzee neonates are born with the ability to match visually perceived oral gestures with a proprioceptive motor scheme (Meltzoff & Moore, 1977, 1983, 1997).

The neonatal imitative behavior of young humans and chimpanzees is probably an expression of an innate adaptive ability resulting from natural selection. Neonatal imitation might play a crucial role in attracting caretaker attention and increasing opportunities for social interaction, which might result in a longer time spent taking care of the neonate, as compared to that initiated merely by crying or simply making a face. Human infants are not unique among primates in their ability to engage, face-to-face, with others; chimpanzee mothers, both in the wild and in captivity, also engage in face-to-face interactions with their infants (Plooij, 1984; Bard, 1994; Bard, Myowa-Yamakoshi, Tomonaga & Quinn, 2002).

Another finding was that the chimpanzees' imitative responses disappeared after 9 weeks of age. It is important to consider why the imitative response declined at around this age. At approximately 2 to 3 months of age, human behavior changes remarkably and infants begin to vocalize and smile spontaneously at others during face-to-face social communications (Field, Goldstein, Vega-Lahr & Porter, 1986; Butterworth & Harris, 1994). Similarly, we found that, at around 9 weeks of age, the infant chimpanzee began to perform mouth opening very frequently, regardless of the facial gesture presented. This response could be considered to be 'social smiling' (i.e. a play face) directed at the human experimenter. We asked several chimpanzee researchers familiar with chimpanzee facial expressions to judge whether these mouth openings could be considered as smiling behavior. They judged that the mouth opening around this age was highly similar to a smiling response.

Bard *et al.* (2002) observed the same mother–infant pairs during the infants' first 3 months of life. In their daily interactions, the mothers and infants engaged in face-to-face interactions, including mutual gaze. It is noteworthy that, at around 8 weeks of age, the level of mutual gaze increased dramatically for these chimpanzees, which suggests that the infant chimpanzees increased their daily face-to-face interactions with their mothers and with others at this time.

As mentioned in the Introduction, Meltzoff and Moore (1992) explained the disappearance of imitative responses in 2-month-olds as due to the fact that older infants respond to people by engaging in social interactions more spontaneously than do neonates. The infant chimpanzees might actively open their mouths as a way to smile and to communicate with other individuals. The developmental change in neonatal imitation seems closely connected with these kinds of social communicative behaviors.

We must also consider whether chimpanzees' facial and bodily imitations reappear as they age. Little research, to date, has addressed the issue of developmental imitative capacity in chimpanzees during early infancy. Studies investigating imitative ability in chimpanzees older than 4 or 5 years have shown that the fidelity of chimpanzee imitation, including facial expressions, whole body movements and manipulation of objects, is less than that in human children (Hayes & Hayes, 1952; Tomasello, Davis-Dasilva, Camak & Bard, 1987; Nagell, Olguin & Tomasello, 1993; Custance, Whiten & Bard, 1995; Myowa-Yamakoshi & Matsuzawa, 1999; Whiten, 1996). It has been shown that adult chimpanzees can immediately imitate demonstrated actions in only 5.4% of trials (Myowa-Yamakoshi & Matsuzawa, 1999). We may conclude from this that chimpanzee imitation is less accurate than human imitation and that the imitative ability of chimpanzees probably develops differently to that of humans.

In conclusion, the capacity for neonatal imitation is a characteristic that is common to humans and chimpanzees. However, the ability to imitate a broad range of whole-body actions or facial expressions is probably an attribute that evolved after the human lineage separated from that of chimpanzees. We propose that, in chimpanzees, the mechanism of neonatal imitation differs from that of later imitation, which appears at approximately 8 to 12 months of age in humans (Myowa-Yamakoshi, 2001). Meltzoff (1996) insisted that imitation is a foundation for understanding others as psychological beings with mental states such as beliefs, emotions and intentions (i.e. 'theory of mind'; Premack & Woodruff, 1978). It is possible that chimpanzees' difficulty at later imitation reflects differences in the development of the mind in the two species.

Further studies are needed to investigate the development of imitative behavior in chimpanzees, especially during infancy, and to determine which characteristics are shared and which differ among humans and chimpanzees from an evolutionary perspective. In addition, we should determine whether other apes and monkeys share early imitative abilities with humans and chimpanzees. Both phylogenetic and ontogenetic comparisons will help to explain why humans have evolved unique imitative abilities.

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