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Comparative cognitive development

Tetsuro Matsuzawa

Primate Research Institute, Kyoto University, Japan

Abstract

This paper aims to compare cognitive development in humans and chimpanzees to illuminate the evolutionary origins of human cognition. Comparison of morphological data and life history strongly highlights the common features of all primate species, including humans. The human mother–infant relationship is characterized by the physical separation of mother and infant, and the stable supine posture of infants, that enables vocal exchange, face-to-face communication, and manual gestures. The cognitive development of chimpanzees was studied using the participation observation method. It revealed that humans and chimpanzees show similar development until 3 months of age. However, chimpanzees have a unique type of social learning that lacks the social reference observed in human children. Moreover, chimpanzees have unique immediate short-term memory capabilities. Taken together, this paper presents a plausible evolutionary scenario for the uniquely human characteristics of cognition.

The human as a primate species

The human mind is an evolutionary product. So is the human body, society, and genome. *Homo sapiens* is one of the 220 or so primate species. The comparison of the human primate with the other primate species may be the best way to understand human nature and to answer questions such as: What is uniquely human? Where did it come from? These are the questions that comparative cognitive science tries to answer.

Recent advances in the study of the human and chimpanzee genome (The Chimpanzee Sequencing and Analysis Consortium, 2005) revealed that the two species are very close. The difference in the DNA level is only 1.23%. In other words, we are 98.77% chimpanzees. The genomic difference between the two species is comparable to that of horses and zebras which differ by about 1.5%.

A comparison of physical aspects of humans and nonhuman primates can also help illustrate the unique features of humans. Table 1 shows the parameters such as adult body mass, neonatal body mass, adult brain mass, neonatal brain mass, gestation period (intrauterine life), weaning, reproductive maturity, and life span. While it is well known that the human has a large brain (about three times as large as that of chimpanzees), the following three points are also worth noting.

First, *the postnatal growth of the brain is roughly the same in humans and chimpanzees*. The neonatal brain of the two species triples in size on reaching the adult level (3.26 times in humans and 3.20 times in chimpanzees). This means that chimpanzees could have similar cognitive developmental changes to humans. Humans learn through experience during postnatal development, as do chimpanzees. The cognitive world of infant chimpanzees is different from that of juveniles, adolescents, and adults. This is why we need to study not only chimpanzee cognition, but also the development of cognition after birth (Matsuzawa *et al.*, 2006).

Second, *humans do not have a large brain if body size is also considered*. The adult body size shows clear sexual dimorphism, and also shows huge individual difference. Therefore, let us focus on the brain size and body size at birth. Table 1 gives the neonatal brain/body mass ratio. As the indices show, there is not much difference among the primate species, including humans (within the range of 0.07 to 0.12). Of course, the absolute volume of brain may be important and critical in cognitive processing. However, it is also possible to down-size while keeping the same function. For example, a recent survey in the caves of Flores islands in Indonesia reported the new hominid record, *Homo florensiensis*. They are estimated have survived until only 18,000 years ago. The fossil hominid, Flores man, was about 1 m high and had only 500 ml brain capacity, comparable to that of the chimpanzee brain. However, there was evidence that they used complex tools and also fire (Brown, Sutikna, Morwood, Soejono, Jatmiko, Saptomo & Due, 2004). Thus, the absolute volume of brain may not be the critical factor for determining cognitive function. This view is also supported by recent studies showing that capuchins' behavior is comparable to that of apes in many respects (Fragaszy, Visalberghi & Fedigan, 2004a). Capuchins show lots of

Address for correspondence: Tetsuro Matsuzawa, Primate Research Institute, Kyoto University, 41 Kanrin, Inuyama, Aichi, 484-8506, Japan; e-mail: matsuzaw@pri.kyoto-u.ac.jp

Table 1 *Characteristics of human growth in primate perspective*

Species	Human	Chimpanzee	Gorilla	Orangutan	Gibbon	Macaque	Capuchin	Lemur
Scientific name	Hs	Pt	Gg	Pp	Hl	Mf	Ca	Lc
Body mass, male (kg)	48	42	160	69	6	12	3	2.9
Body mass, female (kg)	40	31	93	37	5	9	2	2.5
Neonatal body mass (g)	3300	1756	2110	1728	411	503	248	88
Adult brain mass (g)	1250	410	506	413	108	109	71	25
Neonatal brain mass (g)	384	128	227	170	50	55	29	9
Adult/neonatal brain mass ratio	3.26	3.2	2.23	2.43	2.16	1.98	2.45	2.78
Neonatal brain/body mass ratio	0.12	0.07	0.11	0.1	0.12	0.11	0.12	0.1
Gestation period (days)	267	228	256	260	205	170	160	135
Weaning (days)	730	1460	1583	1095	730	182	270	105
Reproductive maturity (months)	198	118	78	84	108	60	43	10
Life span (years)	60	42	39	50	32	25	40	27

Note: Hs: Homo sapiens, Pt: Pan troglodytes, Gg: Gorilla gorilla, Pp: Pongo pygmaeus, Hl: Hylobates lar, Mf: Macaca fuscata, Ca: Cebus apella, Lc: Lemur catta.

combinatorial object manipulation, as do chimpanzees (Fragaszy & Adams-Curtis, 1991; Matsuzawa, 2001; Torigoe, 1985). Recent studies have reported that wild capuchins, adapting to arid habitats, lived on hard-shelled nuts and used a stone tool to crack open the palm nuts just like chimpanzees (Fragaszy, Izar, Visalberghi, Ottoni & de Oliveira, 2004b), and are also good at the collaboration task (Hattori, Kuroshima & Fujita, 2005).

Third, *physical separation of mother–infant right after birth is a unique feature of humans* (Matsuzawa, 2006). Human infants can be stable in the supine posture while the great ape infants cannot. The human infant is fatty (about 20% fat, possibly as an adaptation to the cold temperature at ground level), while the chimpanzee infant is not fatty (about 4% fat). Human mothers do not always carry their infants, while chimpanzee mothers continue to hold their infant 24 hours a day for at least the first 3 to 4 months. Weaning is also earlier in humans in comparison to chimpanzees and other great apes. Chimpanzee infants suck the nipples until they are at least 4 to 5 years old. The average inter-birth interval is about 5 to 6 years in chimpanzees. This means that chimpanzee infants monopolize the mothers for at least the first five years. Thus a long socialization process is not uniquely human, but is unique to the hominoids. Instead, humans are characterized by the physical separation of the mother–infant diad.

In sum, the existing data on human morphology and life history demonstrate the following three important points. First, that developmental change should be explored to understand the nature of cognition in nonhuman primates. Second, nonhuman primates that have smaller brain volume may have developed unique cognitive skills which are adaptive to their own way of life. Third, that the mother–infant relationship is somehow unique in humans in terms of physical separation and early weaning compared to other hominoids.

Cognitive development in infant chimpanzees

Chimpanzees are the closest relative of humans. Since Wolfgang Koehler carried out his pioneering work about 100 years ago, numerous studies have examined chimpanzee cognition in captivity with regard to such capacities as tool use, insightful problem-solving, and rudimentary forms of collaboration. The typical method is called 'cross-fostering', that is, the raising of a chimpanzee infant by a human surrogate. I personally had the experience of raising an infant chimpanzee who was rejected by her mother, at home with my infant daughter. The two infants look alike in many ways. However, I note that it is unfair to compare the two species in such conditions, because, my daughter had her parents whereas the chimpanzee had no parents at all. Chimpanzee infants really need affectionate bonds. Once separated from the mothers, they make a desperate effort to adapt to their human surrogate and human environment. Therefore, it is not surprising that they acquire some human ways of communication such as gestural signs (Gardner & Gardner, 1969). Many previous studies have demonstrated the flexibility of cognitive functions of the isolated apes. However, given the social needs of the developing chimpanzee, it might be time to stop such cruel studies.

My colleagues and I have developed a new way of studying cognitive development in chimpanzees (Matsuzawa *et al.*, 2006) called 'Participation Observation'. The chimpanzee infants were raised by their biological mothers. We had three pairs of mother–infants in the year 2000. They were the members of a community of 14 chimpanzees consisting of three generations living in an enriched environment. Thanks to the long-term relationship between the mothers and the human researcher, we can test the cognition of infant chimpanzees with the assistance of the mother chimpanzees.

A series of cognitive experiments revealed the similarity between humans and chimpanzees in the following ways: Chimpanzee neonates, just like human neonates, showed neonatal smiling (Mizuno, Takeshita & Matsuzawa, 2006). Neonatal smiling is characterized by the eyes remaining closed. Neonatal smiling disappears in the first 2 to 3 months of life. As in humans, it was replaced with the social smiling that is characterized by the eyes remaining open. Chimpanzees also showed facial imitation as humans do (Meltzoff & Moore, 1977; Myowa-Yamakoshi, Tomonaga, Tanaka & Matsuzawa, 2004). The neonatal imitation lasted for the first 2 to 3 months of life, then disappeared, just as it does with humans. Chimpanzee infants preferred a straight gaze rather than an averted gaze (Myowa-Yamakoshi, Tomanaga, Tanaka & Matsuzawa, 2003), and could utilize the gaze cues (Okamoto, Tomonaga, Ishii, Kawai, Tanaka & Matsuzawa, 2002). Mutual gaze is also marked between mother and infants (Bard, Myowa-Yamakoshi, Tomonaga, Tanaka, Costall & Matsuzawa, 2005). Face recognition is one of the key issues of cognitive development in humans (Johnson & Morton, 1991). In parallel to their gaze preference, chimpanzees also developed a preference for their mother's face (Myowa-Yamakoshi, Tomonaga, Tanaka, Costall & Matsuzawa, 2005). In the first month of life, the chimpanzee infants did not show any special preference for their own mother's face. However, they developed a significant preference for their mother's face at 1 to 2 months old. The preference later disappeared. In sum, cognitive development in infant chimpanzees less than 3 months old looks similar to humans in many respects (Tomonaga, Tanaka, Matsuzawa, Myowa-Yamakoshi, Kosugi, Mizuno, Okamoto, Yamaguchi & Bard, 2004).

Infant chimpanzees start to move away from their mother for brief periods at around 3 to 4 months old. They start exploring the outer world, and start interacting with other members of the community at this point. Chimpanzee infants first show object-object manipulation, the precursor of tool use, at the age of 10 months old (Hayashi & Matsuzawa, 2003). The first tool use, using a probing tool to get honey through a small hole, was recorded at slightly earlier than 2 years old (20 to 22 months old) in the three infants (Hirata & Celli, 2003).

Participation observation revealed that the developmental change in object manipulation and tool use corresponds to that observed in their natural habitat (Biro, Inoue-Nakamura, Tonooka, Yamakoshi, Sousa & Matsuzawa, 2003; Humle & Matsuzawa, 2002; Inoue & Matsuzawa, 1997; Matsuzawa, 1994, 1999). Tool use can be classified into several levels by focusing on how the objects are related among each other (Matsuzawa, 1997). At around 2 years old, wild chimpanzees show 'Level 1 tool use', relating one object to another, such as ant-fishing, algae-scooping, and use of leaves for drinking water. At around 4 years old, they start to show 'Level 2 tool use', relating three objects in a hierarchical fashion, such as using stone tools for nut-cracking. For example, the chimpanzees in Bossou, Guinea, West Africa, use a pair of stones as a hammer and anvil to crack open oil palm nuts. They place a nut on the anvil stone, and then hit it with a hammer stone to crack the hard shell and get the edible kernel (Figure 1). At around 6 years old, they develop 'Level 3 tool use', relating four objects in a hierarchical order, such as the use of a wedge stone to stabilize the anvil stone, where the nut is placed, and then hitting the nut with a hammer stone. However, there is no evidence that the chimpanzees can reach Level 4 tool use. There is a limit to how many objects can be combined in the hierarchical order. In contrast, humans can develop hierarchical combinatorial manipulations in infinite levels. Human technology is characterized by the self-embedding and recursive structure of tool use (Hayashi, 2007; Matsuzawa, 1991, 1997).

In sum, chimpanzees show similar cognitive development to humans. However, the developmental process is different from humans in some respects. The following sections will focus on the unique features of chimpanzee cognition in comparison to humans.

Education by master–apprentice

Laboratory studies and field studies together have revealed a unique kind of social learning in chimpanzees. This set of behavioral characteristics was named 'Education by master–apprenticeship' (Matsuzawa *et al.*, 2001). There are three main points: (1) prolonged exposure based on the mother–infant bond, (2) no teaching (no formal instruction, and no positive/negative feedback from the mother), and (3) intrinsic motivation of the child to copy the mother's behavior.

Let us consider stone tool use as an example of social learning. First, the social learning is based on the mother–infant bond because the infant chimpanzees are always carried by their mothers. It is the mothers who provide the learning context. It is important to note that learning does not depend on observing any single case. There are lots of similar cases in daily life. Infants accumulate the experience of observing these similar cases. A prolonged pre-exposure to the nut-cracking situation may be important for the later emergence of imitative processes in the chimpanzee infants.

Second, there is no overt teaching behavior in chimpanzees. Human mothers may mold the hand of the child to teach her how to hold the hammer stone or the way of hammering. She may give a good nut to be cracked or a good stone as a hammer. She may stabilize the anvil

Figure 1 *Chimpanzees at Bossou, Guinea, West Africa, use a pair of stones as hammer and anvil to crack open oil-palm nuts (Photo by E. Nogami).*

stone and put a nut on it to make the nut-cracking easier. However, this is not the case in chimpanzees (although Boesch & Boesch-Asherman, 2000, report two such anecdotal cases in their long-term study lasting more than 10 years). In conclusion, field observations show that chimpanzee mothers in the wild do not teach as human mothers do.

Let us look at this from a different perspective, that is, from the viewpoint of the infant chimpanzees. Consider a human child facing the nut-cracking task. A human child may look at their mother before starting nut-cracking. The human mother may look at the infant to see what is going on. If the human child succeeds in opening the nut, then the child may look back at the mother to show his/her success. The child may smile to the mother and the mother smiles back. However, this is not the case in chimpanzees. There is a triadic relationship in humans: Mother, infant, and object. However, chimpanzee behavior lacks such a triadic relationship. The chimpanzees carefully observe others' behavior, and it may help their own attempt (Hirata & Morimura, 2000; Ueno & Matsuzawa, 2005); however, their problem-solving is based only on direct and dyadic subject–object relationships, not on a social reference framework.

Third, infant chimpanzees have very strong intrinsic motivation to copy their mother's behavior. Chimpanzee infants would start to manipulate the nut or the stone at less than 1 year old; touching, mouthing, pushing, etc. At around 2 years old, they start to combine several objects in various ways, stacking, pushing one on the other, etc. (Inoue & Matsuzawa, 1997). All these attempts do not result in obtaining the edible kernel because the hard shell is not cracked. Moreover, infant chimpanzees are allowed to steal the kernel from the mothers. The mother cracks open the nut and the infant gets the kernel. We know of a case in which the kernels were stolen by an infant seven consecutive times. Simple learning theory may predict the increase of this behavior as it was reinforced by the edible item. However, the stealing behavior actually decreased and the infant continued her effort of combining the nuts and the stones in a proper order. As described, food sharing is common between mother and infant in chimpanzees (Ueno & Matsuzawa, 2004). The infant takes the food from the mother, and not the reverse. However, human infants often try to put an edible item to the mouth of their mother or other persons. This phenomenon has never been observed in chimpanzees. Chimpanzee food sharing is one-way (or unilateral), while in humans it is two-way (or bilateral). Reciprocity may be the key difference between humans and chimpanzees.

Each chimpanzee community in the wild has its own unique cultural tradition (Whiten, Goodall, McGrew, Nishida, Reynolds, Sugiyama, Tutin, Wrangham & Boesch, 1999). Through education by master–apprentice, chimpanzees seem to pass the values, knowledge, and skills from one generation to the next. It must be noted that there might be a sort of critical period in the social learning described above. There are three chimpanzees in the Bossou community who did not crack open nuts. Two of them were thought to be immigrant females who were not exposed to the learning situation of nut-cracking when they were young. One juvenile female was trapped by a wire snare at the foot, and had little opportunity to manipulate the stones and nuts in the important period (Matsuzawa, 1994).

The trade-off between memory and language

This section will focus on the limits and also the unique aspects of chimpanzee cognition. There have been several ape-language projects (Gardner & Gardner, 1969; Premack, 1971; Savage-Rumbaugh, Murphy, Sevcik, Brakke, Williams & Rumbaugh, 1993; Terrace, 1979). It is clear that the chimpanzees and other great apes can master the language-like skill to some extent. They can learn the use of symbols, such as ASL, plastic signs, or letters, to represent each object, color, number, and so on. However, the limitation of their ability also becomes clear. The number of signs or 'words' learned was several hundred at most and never exceeded 1000. The mean length of 'utterances' (MLU) was less than 2: This means that they often used single signs only. There is no clear evidence of syntactical rule use so far.

Chimpanzee Ai is the first chimpanzee to master the use of numerals to represent number (Matsuzawa, 1985, 2003). She learned to touch Arabic numerals in ascending order (Biro & Matsuzawa, 1999, 2001). This skill was used to test her numeric memory span (Kawai & Matsuzawa, 2000). Five numerals, such as 2, 4, 5, 7, and 9, appeared in random positions on the monitor. When she touched the first numeral, the other numerals on the screen turned to white rectangles. However, she was able to touch the rectangles in the correct order. For this task, the chimpanzee had to memorize the numerals and their respective positions before she made the first touch. Chimpanzee Ai was able to do this at the same accuracy level and much quicker than human subjects.

In a recent study by Inoue and Matsuzawa, we taught this numeric memory skill to all of the three mother–infant pairs in PRI, Kyoto University and found that all chimpanzees can master the skill. Thus Ai is not an exceptionally bright chimpanzee. In general, the performance of infant chimpanzees was better than that of their mothers, and also better than human adults (Figure 2a, b). Why do chimpanzees have better immediate memory than humans? Our interpretation is as follows. The common ancestor of humans and chimpanzees may have had the same kind of memory skill. However, in the course of human evolution, we lost the skill while we acquired other language-related skills: representation, chunking, hierarchical organization, syntactic rules, etc. Brain volume capacity was limited at a certain point in evolution, so we had to lose some function to get a new function.

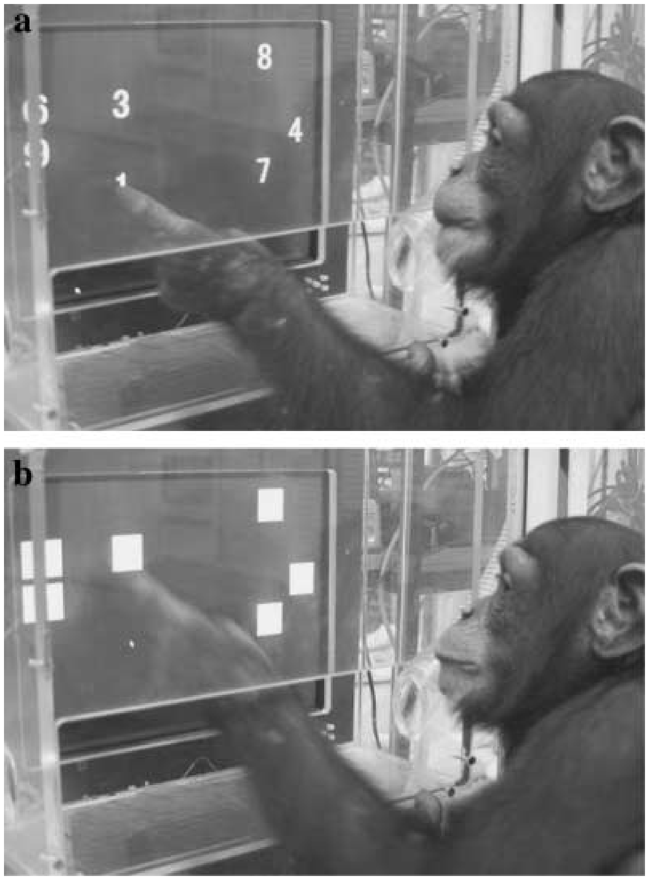

Figure 2 *A test of numeric memory span was applied to a 5-year-old chimpanzee named Ayumu. He can memorize the numerals, that is, which numeral appeared in which position.*

Previous studies revealed that there are some other cognitive tasks in which chimpanzee performance exceeds human performance. Chimpanzees are good at identifying pictures of faces presented upside down, while this is very difficult for humans (Tomonaga, Itakura & Matsuzawa, 1993). Chimpanzees are also good at voice–face matching-to-sample tasks, in which a chimpanzee voice was presented as a sample and then the subject had to choose the photo of the vocalizer from among the alternatives. This is also a very difficult task for human subjects (Izumi & Kojima, 2004). In sum, chimpanzees are good at tasks that seem to have ecological validity for them.

What is uniquely human?

This paper has summarized recent progress in the study of chimpanzee cognition, focusing on developmental change. Cognitive development in chimpanzees can illuminate the unique features of human cognition and its developmental change. This last section will discuss an evolutionarily plausible scenario for the emergence of unique aspects of human cognition.

Let us look at the evolutionary stages of mother–infant relationships. Among mammals, primates developed a unique mother–infant relationship, clinging and embracing (Ross, 2002; Matsuzawa, 2006). Primates had four limbs to grasp objects because they had adapted to the arboreal life. Then, based on the continuous ventro-ventral contact, mutual gazing and smiling developed in the common ancestors of humans and chimpanzees.

The physical separation of mother–infant right after birth is unique to humans. Humans are the terrestrial hominoids who have adapted to the savanna, where the day–night temperature difference becomes large. In the forest, the temperature on the ground is only 1 to 2 degrees lower than that of the canopy. Thick fat in the human infant might be an adaptation to both the environment and the mother–infant separation. Human mother–infant separation resulted in the facilitation of vocal exchange, and the stable supine posture of the infants provided freedom of limb movement. Through these changes, humans developed a unique way of communicating, incorporating multiple sources of signals such as facial expressions, manual gestures, and vocalization (Matsuzawa, 2006).

The mother–infant separation may be due to the change in their social life. There might be several interrelated factors: division of labor or collaboration by a male and a female, the existence of the helper or the 'grandmother' because of the long post-reproductive period, and the strong pair-bonding turning into the family-type group formation. Allo-mothering, the maternal behavior shown by the members of a group, is often found in primate societies. Then, the allo-mothering tendency and the mother–infant separation were mutually reinforced in humans. This led to the early weaning in humans in comparison to the other hominoids. The early life of the human infant is characterized by a dense social network.

Accumulation of knowledge and technology is the key to modern human life. Based on their genetic background, humans have developed their unique way of education. Not only do mothers and infants bond like chimpanzees, but humans also have the family network, so that there are multiple models nearby. Human infants can acquire skills through true imitation, or generalized imitation, that is not seen in chimpanzees (Myowa-Yamakoshi & Matsuzawa, 1999, 2000). This imitative capacity allows the apprentice to learn skills from even a single instance shown by the master. As described above, overt teaching is also uniquely human.

Humans and chimpanzees share the common intrinsic motivation to copy other individuals. In human cases, this is encouraged by teaching and imitation. This intrinsic motivation, combined with the innovative manner of social learning, may have resulted in the cross-generational transmission of values, knowledge, and technology in humans.

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References

Bard, K., Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., Costall, A., & Matsuzawa, T. (2005). Group differences in the mutual gaze of chimpanzees (*Pan troglodytes*). *Developmental Psychology*, **41**, 616–624.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, **6**, 213–223.

Biro, D., & Matsuzawa, T. (1999). Numerical ordering in a chimpanzee (*Pan troglodytes*): planning, executing, monitoring. *Journal of Comparative Psychology*, **113**, 178–185.

Biro. D., & Matsuzawa T. (2001). Use of numerical symbols by the chimpanzee (*Pan troglodytes*): cardinals, ordinals, and the introduction of zero. *Animal Cognition*, **4**, 193–199.

Boesch, C., & Boesch-Acherman, H. (2000). *The chimpanzees of the Taï forest: Behavioral ecology and evolution*. Oxford: Oxford University Press.

Brown, P., Sutikna, T., Morwood, M.J., Soejono, R.P., Jatmiko, W., Saptomo, E., & Due, R.A. (2004). A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature*, **431**, 1055–1061.

Fragaszy, D., & Adams-Curtis, L.E. (1991). Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, **105**, 387–397.

Fragaszy, D., Visalberghi, E., & Fedigan, L. (2004a). *The complete capuchin: The biology of the genus cebus*. Cambridge: Cambridge University Press.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E.B., & de Oliveira, M.G. (2004b). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, **64**, 359–366.

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

Hattori, Y., Kuroshima, H., & Fujita, K. (2005). Cooperative problem solving by tufted capuchin monkeys (*Cebus apella*): spontaneous division of labor, communication, and reciprocal altruism. *Journal of Comparative Psychology*, **119** (3), 335–342.

Hayashi, M. (2007). A new notation system of object

manipulation in the nesting-cup task for chimpanzees and humans. *Cortex*, in press.
Hayashi, M., & Matsuzawa, T. (2003). Cognitive development in object manipulation by infant chimpanzees. *Animal Cognition*, **6**, 225–233.
Hirata, S., & Celli, M. (2003). Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. *Animal Cognition*, **6**, 235–244.
Hirata, S., & Morimura, N. (2000), Naive chimpanzees' (*Pan troglodytes*) observation of experienced conspecifics in a tool-using task. *Journal of Comparative Psychology*, **114** (3), 291–296.
Humle, T., & Matsuzawa, T. (2002). Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *American Journal of Primatology*, **58** (3), 133–148.
Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool-use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **111** (2), 159–173.
Izumi, A., & Kojima, S. (2004). Matching vocalization to vocalizing faces in a chimpanzee (*Pan troglodytes*). *Animal Cognition*, **7**, 179–184.
Johnson, M.H., & Morton, J. (1991). *Biology and cognitive development: The case of face recognition*. Oxford: Blackwell.
Kawai, N., & Matsuzawa, T. (2000). Numerical memory span in a chimpanzee. *Nature*, **403**, 39–40.
Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature*, **315**, 57–59.
Matsuzawa, T. (1991). Nesting cups and meta-tool in chimpanzees. *Behavioral and Brain Sciences*, **14** (4), 570–571.
Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild. In R. Wrangham, W. McGrew, F. deWaal, & P. Heltne (Eds.), *Chimpanzee cultures* (pp. 351–370). Cambridge, MA: Harvard University Press.
Matsuzawa, T. (1996). Chimpanzee intelligence in nature and in captivity: isomorphism of symbol use and tool use. In W. McGrew, L.F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 196–209). Cambridge: Cambridge University Press.
Matsuzawa, T. (1999). Communication and tool use in chimpanzees: cultural and social contexts. In M. Hauser & M. Konishi (Eds.), *The design of animal communication* (pp. 645–671). Cambridge: Cambridge University Press.
Matsuzawa, T. (Ed.) (2001). *Primate origins of human cognition and behavior*. Tokyo: Springer-Verlag.
Matsuzawa, T. (2003). The Ai project: historical and ecological contexts. *Animal Cognition*, **6**, 199–211.
Matsuzawa, T. (2006). Evolutionary origins of the human mother–infant relationship. In T. Matsuzawa *et al*. (Eds.), *Cognitive development in chimpanzees* (pp. 127–141). Tokyo: Springer: Tokyo.
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.
Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2006). *Cognitive development in chimpanzees*. Tokyo: Springer.
Meltzoff, A.N., & Moore, M.K. (1977). Imitation of facial and manual gestures by human neonates. *Science*, **198**, 75–78.
Mizuno, Y., Takeshita, H., & Matsuzawa, T. (2006). Behavior of infant chimpanzees during the night in the first four months of life: smiling and suckling in relation to behavioural state. *Infancy*, **9** (2), 215–234.
Myowa-Yamakoshi, M., & Matsuzawa, T. (1999). Factors influencing imitation of manipulatory actions in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **113** (2), 128–136.
Myowa-Yamakoshi, M., & Matsuzawa, T. (2000). Imitation of intentional manipulatory actions in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **114**, 381–391.
Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2003). Preference for human direct gaze in infant chimpanzees (*Pan troglodytes*). *Cognition*, **89**, 113–124.
Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2004). Imitation in neonatal chimpanzees (*Pan troglodytes*). *Developmental Science*, **7** (4), 437–442.
Myowa-Yamakoshi, M., Yamaguchi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2005). Development of face recognition in infant chimpanzees (*Pan troglodytes*). *Cognitive Development*, **20**, 49–63.
Okamoto, S., Tomonaga, M., Ishii, K., Kawai, N., Tanaka, M., & Matsuzawa, T. (2002). An infant chimpanzee (*Pan troglodytes*) follows human gaze. *Animal Cognition*, **5**, 107–114.
Premack, D. (1971). Language in chimpanzees? *Science*, **172**, 808–822.
Ross, C. (2002). Park or ride? Evolution of infant carrying in primates. *International Journal of Primatology*, **22**, 749–771.
Savage-Rumbaugh, S., Murphy, J., Sevcik, R.A., Brakke, K.E., Williams, S.L., & Rumbaugh, D. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child Development* (Serial 233), **58** (3–4), 1–254.
Terrace, H. (1979). *Nim*. New York: Knopf.
The Chimpanzee Sequencing and Analysis Consortium (2005). Initial sequence of the chimpanzee genome and comparison with human genome. *Nature*, **437**, 69–87.
Tomonaga, M., Itakura, S., & Matsuzawa, T. (1993). Superiority of conspecific faces and reduced inversion effect in face perception by a chimpanzee. *Folia Primatologica*, **61**, 110–114.
Tomonaga, M., & Matsuzawa, T. (2002) Enumeration of briefly presented items by the chimpanzee (*Pan troglodytes*) and humans (*Homo sapiens*). *Animal Learning and Behavior*, **30**, 143–157.
Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M., Kosugi, D., Mizuno, Y., Okamoto, S., Yamaguchi, M., & Bard, K. (2004). Development of social cognition in infant chimpanzees (*Pan troglodytes*): face recognition, smiling, gaze, and the lack of triadic interactions. *Japanese Psychological Research*, **46** (3), 227–235.
Torigoe, T. (1985) Comparison of object manipulation among 74 species of non-human primates. *Primates*, **26**, 182–194.
Ueno, A., & Matsuzawa, T. (2004). Food transfer between chimpanzee mothers and their infants. *Primates*, **45**, 231–239.
Ueno, A., & Matsuzawa, T. (2005). Response to novel food in infant chimpanzees: do infants refer to mothers before ingesting food on their own? *Behavioral Processes*, **68** (1), 85–90.
Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C., Wrangham, R., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, **399**, 682–685.