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REVIEW

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The Ai project: historical and ecological contexts

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Abstract This paper aims to review a long-term research project exploring the chimpanzee mind within historical and ecological contexts. The Ai project began in 1978 and was directly inspired by preceding ape-language studies conducted in Western countries. However, in contrast with the latter, it has focused on the perceptual and cognitive capabilities of chimpanzees rather than communicative skills between humans and chimpanzees. In the original setting, a single chimpanzee faced a computer-controlled apparatus and performed various kinds of matching-to-sample discrimination tasks. Questions regarding the chimpanzee mind can be traced back to Wolfgang Koehler's work in the early part of the 20th century. Yet, Japan has its unique natural and cultural background: it is home to an indigenous primate species, the Japanese snow monkey. This fact has contributed to the emergence of two previous projects in the wild led by the late Kinji Imanishi and his students. First, the Koshima monkey project began in 1948 and became famous for its discovery of the cultural propagation of sweet-potato washing behavior. Second, pioneering work in Africa, starting in 1958, aimed to study great apes in their natural habitat. Thanks to the influence of these intellectual ancestors, the present author also undertook the field study of chimpanzees in the wild, focusing on tool manufacture and use. This work has demonstrated the importance of social and ecological perspectives even for the study of the mind. Combining experimental approaches with a field setting, the Ai project continues to explore cognition and behavior in chimpanzees, while its focus has shifted from the study of a single subject toward that of the community as a whole.

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Introduction

I have been studying the cognition and behavior of chimpanzees both in the field and in the laboratory (Matsuzawa 2001a). My partner in the laboratory study has, for more than two decades, been a female chimpanzee named Ai. Since the age of 1 year, Ai has learned a multitude of skills, including the use of visual symbols. Ai gave birth to a male infant in 2000. Two other females in Ai's group gave birth in the same year. This brought the size of the community to a total of 15 chimpanzees: three generations of individuals 0- to 37-years-old, including three mother–infant pairs. This captive group has thus come to resemble the wild community at Bossou, which currently consists of 19 chimpanzees of three generations. By carrying out cognitive studies in our twin facilities – one in the laboratory and another in the wild – the Ai project's aim since 2000 has been to clarify aspects of the chimpanzee mind within social contexts, focusing specifically on the emergence, modification, and cross-generational transfer of cultural traditions in chimpanzee communities. This paper aims to review the Ai project in the framework of the development of primatology, especially socio-ecological studies, in Japan.

Japan has its own indigenous species, Japanese monkeys, *Macaca fuscata*, also known as "snow monkeys". In contrast, there are no monkeys native to North America and Europe. Japanese children grow up with a rich folklore and many fairy tales in which monkeys play a key role. Thanks to the natural environment and cultural traditions, the study of nonhuman primates in Japan has its own unique history – yet its development took place under a continuous influence from Western thought of the same era. By looking back through the past, the direction that a future controversy on the chimpanzee mind might take becomes clear: what should be explored and how should it be done? To contribute to this debate, the present review article attempts to recount the Ai project from historical and ecological perspectives.

Study of wild Japanese monkeys since 1948

The day was 3 December 1948. World War II had been over for just 3 years. Kinji Imanishi (1902–1992) set off with two of his students, Shunzo Kawamura (1924–2003) and Jun'ichiro Itani (1926–2001) to Koshima Island where they were to begin a long-term study of wild Japanese macaques. Imanishi was 46 years old at the time, a lecturer at the Department of Zoology of Kyoto University. Kawamura and Itani were both undergraduate students. Imanishi, had started out as a fieldworker in entomology, and had discovered the phenomenon of "habitat segregation" (focusing on four species of mayfly larvae in the same stream) in the 1930s. He expanded the idea to characterize evolution as the noncompetitive coexistence of various kinds of organisms as a whole (Imanishi 2002).

Imanishi and his students began their fieldwork by observing the behavior of wild Japanese monkeys, giving nicknames to all the individuals in order to identify each one uniquely. Their target was to unravel the social structure of the groups, as a way of seeking the evolutionary origins of human society. Imanishi organized a research team of ten people, including himself, who visited 19 research sites in Japan – Takasakiyama, Koshima, Arashiyama, and Yakushima among them – to study wild populations of Japanese monkeys. By 1955, during the first 7 years of the study, they had sent out about 90 parties and spent a total of about 1,500 days observing the wild monkeys.

Their attempt was so unique that they succeeded to uncover various hitherto unknown aspects of the monkeys' social behavior. Among their most important findings were the following. One, the monkeys lived in a community called a "troop" that consisted of multiple males and multiple females and moved from place to place as a whole. Two, they had a matrilineal society. The researchers found that all of the solitary monkeys were male. Males grew up and migrated to other communities, while females remained in their natal group. Three, neighboring communities were separate, exclusive entities. Over the years, a group could split into two different communities but not the reverse. Four, members of the group were ranked according to their standing in society. Some individuals were dominant, as were certain family lines, while within the same matrilineal family, the youngest individual was more dominant than the older siblings – a phenomenon known as "Kawamura's law". Five, Itani (1963) recognized that the monkeys had a set of distinctive vocalizations. He identified six groups of 37 different vocal sounds, such as coo calls and alarm calls, emitted in different social contexts.

Among the numerous findings of Imanishi's team, the best known is the cultural propagation of sweet-potato washing. Sweet-potato washing (SPW) is a behavior in which monkeys take a sweet potato to the edge of the water and wash the sand off it with water (Fig. 1). This behavior was first seen in the summer of 1953, performed by a female named Imo ("potato" in Japanese) who was 1.5 years old at that time. The initial observation was made by Satsue Mito (1920–), a local collaborative researcher.

Fig. 1 Sweet-potato washing. Japanese monkeys on Koshima island take a potato to the edge of the water and wash the sand off it. This behavior began in September 1953 by a female named Imo (meaning "potato" in Japanese), 1.5 years old at the time. The behavior gradually spread to the other monkeys (Photo by K. Watanabe)

Mito and her father had been dedicating themselves to the conservation of wild monkeys in Koshima as "national heritage existence". The finding was first reported by Kawamura in 1954 in Japanese. English-speaking readers will be more familiar with Masao Kawai's (1924–) follow up, widely cited paper, which describes the propagation process in detail, along with reports of three other newly acquired behaviors: wheat placer mining behavior, snatching behavior, and bathing behavior (Kawai 1965). Cultural propagation among Koshima monkeys is a topic recently revisited by Kawai and his young colleagues (Hirata et al. 2001a).

The SPW behavior gradually spread to other members of the community. The first 5 years' records show that the acquisition rate in adults more than 8 years old was only 18% (2 out of 11). Both were females. None of the adult males ever performed this practice. The rate in young monkeys aged between 2 to 7 years old was much higher: 79% (15 out of 19) acquired the behavior. After that, most newborns began to show SPW behavior. In sum, the younger generation was sensitive toward the new invention, while adults rarely adopted the behavior.

The propagation process was clear, involving two main channels: through kinship and through playmate relations. In the 4th year following the invention, ten individuals including Imo performed the SPW behavior. One route of transmission was along the family line: after Imo's invention, the mother (Eba) adopted the SPW behavior in the same year. Imo's brother, Ei, younger by 2 years, took up SPW at the age of 1–1.5 years. The other route led to Imo's playmates. All seven remaining individuals were Imo's playmates, no more than a year younger or older, and acquired the skill at the ages of 2–5 years. These data also suggest a critical period for learning SPW.

The SPW behavior became fixed in the troop during the years 1958–1959. By this time almost all infants were acquiring the skill. The Koshima troop also has another cultural behavior called "wheat placer mining" (WPM), which resembles gold mining. For provisioning, researchers scattered grains of wheat around the beach. At first, monkeys ate them by picking up one grain after another – a time-consuming effort. Then, one monkey began to gather up the grains of wheat together with some sand, took them to the shore, and threw them into the water. The advantage of this method was clear: water easily separated the grains from the sand, and while the latter sank to the bottom, the grains floated to the surface.

The inventor of this behavior, first observed by Kawamura in 1957, was once again Imo. The propagation process for WPM was similar to that observed for SPW: through family lineage and playmate relations. Kawai and his colleagues conducted intensive follow up studies. An interesting case was that of "pool-making", which was especially efficient for WPM behavior. When grains of wheat remained scattered on the beach while it was still wet at low tide, some monkeys dug into the sand, creating small pools from the water that oozed up. They then dipped a piece of sweet potato or swept nearby grains of wheat into the pool before consuming them. Cultural innovations thus continue to emerge.

Imo, the originator of SPW and WPM, died on 21 May 1972. She was 20 years old, the average life span of a Japanese monkey, having given birth to six sons and three daughters. Long-term study at Koshima still continues. It is now in its 6th decade, and has recorded the history of eight generations of wild monkeys (Watanabe 2001, personal communication). None of the monkeys who experienced the emergence of these particular cultural behaviors are alive at present. However, their descendants are still dipping sweet potatoes into the sea, and throwing grains of wheat into the water. The behaviors have been transmitted over several generations.

Study of wild chimpanzees since 1958

The day was 4 February 1958. Imanishi and Itani arrived in Nairobi, Kenya. After 10 years accumulating knowledge of Japanese monkeys, they were now to begin working on the African great apes in the wild. In search of a good research site, they went on to visit Tanzania, Uganda, Zaire, Congo and Cameroon. They initially focused on gorillas, not chimpanzees. They first encountered wild mountain gorillas in Uganda and lowland gorillas in Cameroon.

Fig. 2 Wild chimpanzees in the Mahale mountains, Tanzania (Photo by J. Itani, 1971)

On the way back from Africa, the two visited various European countries as well as the United States, carrying with them a film of wild Japanese monkeys in Koshima and the first volume of *Primates*, the international journal of primatology they founded. They met Clarence Carpenter and other distinguished scholars and opened a window to the West.

Since that time, Imanishi, and later Itani, continued to send graduate students to Tanzania, East Africa each year. Among them, Kosei Izawa (1939–) reached the Mahale Mountains in 1965, and Toshisada Nishida (1941–) succeeded to provision the Mahale chimpanzees in 1966 (Fig. 2). Research at Mahale in Tanzania – a site as well known as Gombe (Goodall 1986) – is now in its 37th year (Nishida 1990). Japanese scientists have also been operating another great ape research site: at Bossou, Guinea, West Africa. Bossou was discovered as an important chimpanzee field site by the French Zoologist M. Lamotte in 1942. Later, Dutch scientists including Adrian Kortlandt carried out brief surveys lasting up to a couple of weeks in 1965, 1967, and 1969 (Kordlandt 1986; Kordlandt and Holzaus 1987). Finally, Yukimaru Sugiyama (1935–) arrived at the site in 1976 and laid the foundations for long-term research (Sugiyama and Koman 1979a). Since then, fieldwork at Bossou has continued for 27 years, and has provided us with valuable information on a unique community of Western chimpanzees (*Pan troglodytes verus*). There are only six major research sites around Africa where long-term study of chimpanzees has been carried out: Gombe, Mahale, Bossou, Kibale, Budongo, and Tai (Boesch and Boesch-Achermann 2000). Two of these, Mahale and Bossou, have been run by Japanese researchers, based largely on the efforts of Imanishi and his colleagues.

Imansihi and Itani became the driving force behind the establishment of the Japan Monkey Center (JMC) in 1956. The JMC is a private foundation, an open-air museum and a special zoo exhibiting only nonhuman primates. It has grown to acquire the largest collection of primate species in the world, a total of about 90 species. This was later to help Japanese researchers to carry out unique studies on primate cognition by comparing a large number of species (Torigoe 1985; Kobayashi and Koshima 1997). The JMC first published *Primates*, an English-language journal of primatology, in 1957. The journal is thus the oldest one in the discipline, and continues today with the support, since 2003, of Springer-Verlag.

Based on the accumulation of their achievement, Imanishi and his colleagues succeeded in convincing the Japanese government to found the Primate Research Institute, a national institute for primatology, in 1967. The institute was attached to Kyoto University, a national university to which Imanishi and others belonged. At present, the Primate Research Institute of Kyoto University (KUPRI) has 40 faculty members, many postdoctoral researchers and graduate students, foreign scholars, and about 800 individuals of 20 species of nonhuman primates.

The author is about 50 years younger than Imanishi, and belongs to the second generation in the line of Japanese primatologists. The first generation, Imanishi and his students, strove to establish research sites in the wild. As a spiritual descendant of Imanishi and Itani, I have been developing my own niche of research: the study of the chimpanzee's mind rather than society (Matsuzawa 1985a, 2001a). I have been carrying out long-term research on chimpanzees' cognitive behavior since 1978, in the framework of the so-called Ai project.

Study of the chimpanzee mind since 1978

The day was 30 November 1977. A 1-year-old female chimpanzee arrived at KUPRI, Japan. She was wild-born in the Guinean Forest, which spreads across four countries in West Africa: Guinea, Sierra Leone, Liberia, and Cote d'Ivoire. This means that she was a *verus* chimpanzee (*Pan troglodytes verus*). The infant was purchased through an animal dealer. Importing wild-born chimpanzees was still legal at the time, as Japan only ratified CITES 4 years later, in 1980. In the 1970s, Japan imported more than 100 wild-born chimpanzees, mainly for biomedical research of hepatitis B. This infant chimpanzee was one of them. However, instead of being sent to a biomedical facility, she was sent to KUPRI where she was to become the first subject of an ape-language research project in the country.

The chimpanzee was soon nicknamed "Ai" (pronounced "eye"). Ai means "love" in Japanese, and is also one of the most popular girls' name in Japan. She was estimated to have been born in 1976; hence she was about 1 year old at the time of her arrival. After being examined in quarantine, she was kept in a basement room, only about 4×4 m in size and without any windows. I was 27 years old at the time, the youngest assistant professor in the institute, and was expected to become Ai's principal trainer. I first met her in that dimly lit basement room, with a bulb hanging from the ceiling. When I looked into this chimpanzee's eyes, she looked back into mine. This amazed me – the monkeys I had known and worked with never looked into my eyes. For them, staring straight into one's eyes carried a threat, and they would be likely to respond by opening their mouth and threatening you back or by presenting their back and assuming a submissive posture. I had simply thought that chimpanzees would be big black monkeys. This, however, was no monkey. It was something mysterious.

Soon after Ai's arrival, she was joined by two other infant chimpanzees of around the same age. One was a 1.5-year-old male, named "Akira", and the other a 1.5-year-old female, named "Mari". The construction of the chimpanzee facility had also been completed by this time, and it consisted of four individual residential rooms (1.5×1.5×2 m high) and an attached outdoor pen (about 15m^2). The three infant chimpanzees moved to the new facility.

Historical background of the Ai project

What is uniquely human? This question has long attracted psychologists. Specifically, many have tried to explore the human mind through comparisons with the mind of the chimpanzee (Yerkes 1929; Koehler 1957; Ladygina-Kohts 2002). These efforts were followed up by the work of the Kellogs (a 9-month study in 1931 of an infant chimpanzee named Gua; Kellog and Kellog 1931), the Hayes (a 6.5-year study starting in 1947 of an infant chimpanzee named Vicky; Hayes 1951), and so forth. Then, in the early 1970s, a major turning point arrived in this research area: the beginning of the so-called ape-language studies.

By the second half of the 1970s, three successful and different approaches had been devised to explore the linguistic skills of chimpanzees: American Sign Language (Gardner and Gardner 1969), plastic sign language (Premack 1971), and computer-controlled lexigram system (Rumbaugh et al. 1973). All three projects produced reports that appeared in the journal *Science,* and had received wide attention.

The chimpanzee project in KUPRI began in 1977 with the arrival of the first subject, Ai, to the institute. The project originally had the aim of becoming an ape-language study in Japan. The chimpanzee project in KUPRI was led by Dr. Kiyoko Murofushi, an associate professor and the head of the Section of Psychology at the time. Dr. Murofushi was flanked by three young assistant professors, Toshio Asano, Shozo Kojima, and myself. However, when the project started, Asano was only halfway through a 2-year sabbatical at the University of California, San Diego (UCSD), and Kojima was about to leave for his 2-year sabbatical to the National Institutes of Health, in Bethesda, Maryland (NIH). Therefore, I had to face the three chimpanzees by myself, as the principal trainer/researcher under the supervision of Dr. Murofushi. Having taken up my position at the institute in 1976, I only had very limited experience in experimental psychology: human visual perception, physiological-psychological study of rats' memory, and only a single year's experience with visual discrimination learning in Japanese monkeys.

I had an intrinsic interest in and motivation to study the visual world of nonhuman primates. How do these animals see the world? Is their perception similar to humans'? Such questions were originally proposed by von Uexkuell, a 19th century ethologist, and were first tackled by a new discipline that emerged in the 1960s called "animal psychophysics" (Blough 1961; Stebbins 1970; and others). Instead of concentrating on communication and language in the framework of ape-language studies, I proposed a research plan that was to focus on "the study of the perceptual world of chimpanzees" by applying the discrimination learning paradigm and the assistance of a computer-controlled system.

Prior to starting the project, we had very little experience with chimpanzees. A single female chimpanzee, named Reiko, had been living at the institute since 1968, and had mainly served as the subject for a bipedal locomotion study by morphologists. The only psychological research that had been carried out on the chimpanzee (Asano and Kumazaki 1975) explored an operant response for controlling the lighting in her room. The chimpanzee had a switch with which she could freely turn the lighting on and off, and the researchers recorded the emergent circadian rhythm in the spontaneous switching-on and -off behavior.

Murofushi and her colleagues, consulting experts in related disciplines, endeavored to clarify the goals and methods of the ape-language research, as well as its stance in relation to the ongoing projects in the United States. The consultants included Dr. Kisou Kubota (who majored in neuroscience of the frontal lobe of the brain), Dr. Makoto Nagao (who specialized in computer processing of human natural language, and is the present dean of Kyoto University), and Drs. Akio Kamio and Susumu Kuno (both linguists of generative grammar).

Carefully examining the achievements and methods of the American studies, we set up our own aims and techniques in the following manner. The goal was to study the acquisition process of an artificial language and the corresponding brain mechanisms. Although it became clear that the apes could learn to use visual symbols to some extent, the acquisition process remained unclear. No one had previously tried to connect the psychological facts to brain functions. There were no positron emission tomography (PET), no functional magnetic resonance imaging (fMRI), no magnetoencephalography (MEG), and no magnetic stimulation techniques available at that time. Dr. Murofushi, the leader of the project, was carrying out split-brain research in monkeys in collaboration with Dr. Kubota (Murofushi 1975). But, by this time the notion of performing invasive brain studies with the chimpanzees was already rejected by everyone involved in the discussion, and instead, cranial cooling of a hemisphere was deemed suitable as a noninvasive and reversible technique. However, the technique was never performed in the real project. Instead, we agreed to focus on "the perceptual and cognitive basis of language-like skills" mastered by the chimpanzees. According to my personal perspective, what I truly aspired to do was to explore the perceptual world of chimpanzees through clearly defined visual symbols. My central questions were: How do chimpanzees perceive this world? Do they perceive it like we do? (Matsuzawa 1985a, 1985b)

From among the three existing alternative approaches, we chose to adopt the computer-controlled lexigram system developed by Rumbaugh and his colleagues (Rumbaugh 1977). Our decision was influenced by three factors. First, in the 1970s we had already established sophisticated computer-controlled experiments involving various visual discrimination learning tasks in monkeys (Murofushi 1975; Asano 1976; Kojima 1980; Fujita 1982), such that we were able to immediately apply our existing techniques to the new ape-language research project. Second, we aimed to clarify the acquisition process or underlying perceptual capabilities of language-like skills, which meant that we needed very objective, precise, and detailed records of what we had done and how the chimpanzees behaved. For that purpose, a computer-controlled system was essential for the study. Third, the project had a perspective for future applications of techniques from brain science, and for that purpose we hoped that the subjects would sit quietly on a bench facing the computer system.

The computer system that we had used for monkeys in the 1970s was based on DEC PDP12 and PDP8. However, DEC PDP/V03 soon became available for chimpanzee research. Toshio Asano, in collaboration with technician Sumiharu Nagumo, was in charge of developing the PDP-minicomputer-based system for controlling visual symbols. They originally built an interfacing device for a keyboard with the IEE in-line projectors displaying visual symbols, and also developed a computer program in BASIC programming language. The appearance of the experimental setting was very similar to that invented by Rumbaugh's LANA project (Rumbaugh 1977). Based on published articles from the latter, one could easily replicate the setup, even though we had had no contact to Rumbaugh's group before our project began. Although our apparatus resembled this previous study, our goal was quite different and unique. We were attempting to clarify the acquisition process of the visual symbols and to clearly illuminate the steps involved in complex language-like skills in chimpanzees.

For us, Lana chimpanzee's computer performance seemed to be a sequence of visual discrimination tasks similar to that seen in monkeys. For example, when the chimpanzee touches five keys on the keyboard consecutively, the sequence does not necessarily correspond to a sentence such as "Please/give/Lana/chocolate/period" in human verbal behavior. We were hoping to investigate how specific visual symbols such as those representing the names of individuals, objects, colors, numbers, actions, and so forth, could be established in chimpanzees.

Focus of the Ai project: perceptual and cognitive processes rather than linguistic skills

The day was 15 April 1978. The chimpanzee Ai participated in a computer task inside an experimental booth (2×2×2 m) for the very first time. Her first task was to touch a lit key on the keyboard. Ai was alone inside the testing booth while I, the experimenter, remained outside. There was no direct interaction between the chimpanzee and the human tester. Instead of demonstrations by a model or molding the hands of the chimpanzee, we used the "successive approximation" method for shaping the key-touch behavior. When the subject faced the apparatus, a chime rang and a piece of apple was delivered by a universal food dispenser to a food cup attached to the keyboard. The criterion for delivering the reward was gradually changed, until step-by-step the chimpanzee began to approach the key, then eventually pressed it. Over the years that followed and up to the present day, Ai has continued to press keys and thus to uncover many aspects of chimpanzee intelligence. Throughout the later stages, the Ai project was characterized by a highly automated computer-controlled system without any social interaction during the tests. However, we made sure that a lot of interaction took place during out-of-test play situations, which produced an affectionate tie between the tester and the subject, in turn helping to carry out the tests smoothly.

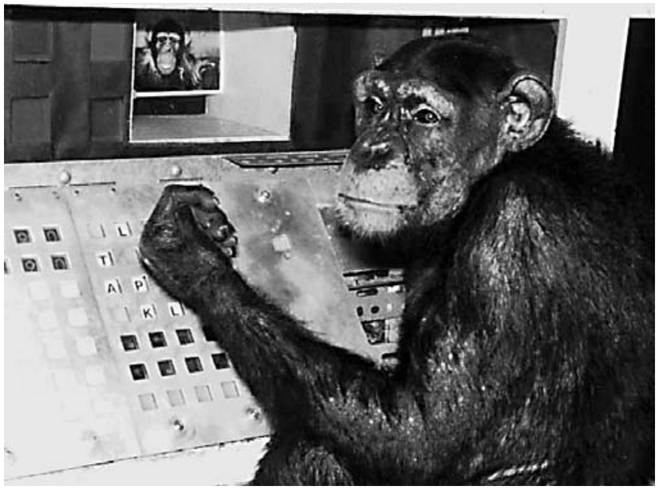

Fig. 3 The original test situation used in the Ai project. The chimpanzee, Ai, is sitting on a bench in front of the keyboard terminal interfaced to a minicomputer (Photo by T. Matsuzawa, 1983)

The first English-language publication about the project appeared in 1982 (Asano et al. 1982). It described our research system, and the process through which the three chimpanzees acquired visual symbols corresponding to object and color names. The visual symbols, uniquely devised by us, became known as the Kyoto University Lexigram system (KUL). In contrast to the Yerkish Lexigram system devised by Rumbaugh and his colleagues, KUL lexigrams had no background color. The lexigrams consisted of black and white patterns and were fundamentally similar to Kanji (Japanese-Chinese characters) that Japanese people use in their daily lives. In addition to the KUL lexigrams, we also used 26 uppercase letters of the alphabet, and Arabic numerals from 0 through 9.

The original keyboard contained three panels. Each panel consisted of 35 keys arranged in seven rows by five columns. The KUL lexigrams were drawn on a film sheet and inserted over the keys. Each key, 1.5×2.0 cm in size, could be back lit, indicating those available in a particular test. Touches to lit keys produced a feedback sound (click), their light faded, and a facsimile of the lexigram appeared on the in-line projectors above the keyboard. There was a display window (20×30 cm) through which the tester showed an object to the chimpanzee, who sat voluntarily on the bench, facing the apparatus (Fig. 3).

The general procedure was matching-to-sample (MTS). In a sense, from the beginning our project was not aimed at becoming another study of language-like or communication-like interactions with the chimpanzees, in the mold of previous studies. Instead, we attempted to clarify the acquisition processes behind such skills and to illuminate the chimpanzees' capability in their matching skills in a very objective way. Hence, our tasks in principle were exact equivalents of the MTS tasks given to other animals – monkeys, rats, pigeons – in the laboratory.

After gathering data on color perception (Matsuzawa 1985b), shape perception and visual acuity (Matsuzawa 1990a), we proceeded to study the recognition of numbers by the chimpanzees. Ai became the first chimpanzee who learned to use Arabic numerals to represent quantities (Matsuzawa 1985a). We still maintain this line of research as a core part of the project, focusing on the perceptual and cognitive capabilities of chimpanzees in comparison with humans and nonhuman primates. The original paradigm of the Ai project was to test single subjects (both humans and chimpanzees participated) facing a computer terminal under identical conditions and using the same apparatus and procedure. This study area is now called comparative cognitive science (CCS) (Matsuzawa 2001b; Matsuzawa and Tomonaga 2001).

The project increasingly covers short-term memory (Fujita and Matsuzawa 1990; Kawai and Matsuzawa 2000), the learning of sequences (Oshiba 1997; Biro and Matsuzawa, 1999; Kawai 2001), visual preference measured by sensory reinforcement (Fujita and Matsuzawa 1986), color classification (Matsuno et al. 2003), the perception of geometric figures (Tomonaga and Matsuzawa 1992), the perception of video images (Morimura and Matsuzawa 2001), the representation of symbols (Kojima 1984; Itakura 1992; Itakura and Matsuzawa 1993), concept of numbers (Matsuzawa 1985a; Murofushi 1997; Tomonaga and Matsuzawa 2000, 2002; Biro and Matsuzawa 2001a, 2001b), the use of tokens (Sousa and Matsuzawa 2001), choice between two discrimination tasks (Suzuki and Matsuzawa 1997), computer-assisted drawing and finger-maze (Iversen and Matsuzawa 1996, 1997, 2001, 2003).

Masaki Tomonaga, my collaborator and junior colleague, developed visual search paradigms rather than discrimination tasks in chimpanzees (Tomonaga 1993a). Using the visual search paradigm, he studied the perception of shape from shading (Tomonaga 1998), visual search asymmetries (Tomonaga 1993a), visual texture segregation (Tomonaga 1999b), perception of biological motion (Tomonaga 2001), global-local processing (Fagot and Tomonaga 1999), action and attention (Tomonaga 2002), and so forth. He also studied face recognition (Tomonaga et al. 1993; Tomonaga 1999a), and the establishment of stimulus equivalence (Tomonaga et al. 1991; Tomonaga 1999c). Masayuki Tanaka, another collaborator, focused on concept formation and categorization (Tanaka 1995, 1996, 2001, 2003). Kazuo Fujita who moved to the Department of Psychology, Kyoto University, explored the visual illusory effects such as the perception of Ponzo illusions (Fujita 1997), and the perception of object unity (Sato et al. 1997). Shozo Kojima and his collaborators have also explored auditory perception and cognition (Kojima and Kiritani 1989; Kojima et al. 1989; Kojima 1990, 1992, 2003a), auditory-visual intermodal matching (Hashiya and Kojima 1997, 2001), identification of vocalizers (Kojima et al. 2003) and body image (Kojima 2003b). The experimental paradigm of "single subject facing to a computer for the perceptual and cognitive tasks" developed at KUPRI continues to offer a unique window on the perceptual and cognitive world of the chimpanzee.

The study of cognition and behavior in chimpanzees by KUPRI researchers has facilitated other research on chimpanzees: locomotion and posture (Kimura 1987, 1991, 1996), physical development (Kimura and Hamada 1996; Hamada et al. 2003; Nishimura et al. 2003), paternity testing based on DNA typing (Takenaka et al. 1993), and the relationship between immunology and dominance (Masataka et al. 1990). It has also aided studies in other facilities, such as zoos, in Japan. These have provided rare opportunities to study cognition and behavior in chimpanzees: tool use and object manipulation (Torigoe 1985), hand preference (Tonooka and Matsuzawa 1993), gaze-monitoring (Itakura 1996), and so forth. Moreover, Japanese scholars have also embarked on research of captive chimpanzees in foreign countries (Takeshita and van Hooff 1996; Takeshita and Walraven 1996).

Field experiments with wild chimpanzees

As previously stated, Japan has an indigenous monkey species while other leading industrial nations have none. This natural precondition has greatly promoted the study of nonhuman primates in Japan. Through my research with the chimpanzee Ai, and probably based on my own natural and cultural background, I felt a necessity to learn about the behavior and the ecological environment of chimpanzees by visiting their natural habitat. I joined the field-study of Bossou chimpanzees in 1986, as the second researcher after Sugiyama, visiting Bossou once or twice a year since then. I have been studying tool manufacture and use, focusing specifically on the developmental processes underlying such skills, and the cultural variation among neighboring communities (Matsuzawa 1994, 1999; Matsuzawa et al. 2001; Biro et al. 2003).

Bossou chimpanzees use a pair of stones as hammer and anvil to crack open oil-palm nuts (Fig. 4) (Sugiyama and Koman 1979b). At Bossou, one can regularly observe five types of tool use (for a review, see Matsuzawa 1999): nut cracking with stones (Humle and Matsuzawa 2001), pestle-pounding of oil-palm trees (Sugiyama 1994), algae scooping with a stick (Matsuzawa 1999), ant dipping using a wand (Humle and Matsuzawa 2002), and the use of leaves for drinking water (Tonooka 2001). In addition to these, new items are added to the tool list each year, some of which are unique to this community: using leaves as cushions (Hirata et al. 1999), capturing and toying with hyraxes (Hirata et al. 2001b), and so on.

Fig. 4 Wild chimpanzees at Bossou use a pair of stones to crack open oil-palm nuts (Photo by T. Matsuzawa)

My colleagues and I have carried out a "field experiment" on tool use in an "outdoor laboratory" located on the top of a hill that forms a core part of the habitat and where chimpanzees are at ease (Matsuzawa 1994; Inoue-Nakamura and Matsuzawa 1997). We provided nuts and stones for nut-cracking, water in an artificially-made tree hollow for leaf sponging, and a regime of oil palm or dead insects to attract Safari ants for ant dipping. The experimental manipulations – such as adding fresh water to the tree hole daily (Tonooka 2001) – had minimal effects on the natural environment, yet succeeded to drastically increase our opportunities to observe tool use from close range and to make video recordings for further detailed analysis. They also provided us with the opportunity to compare different types of tool use performed at the same site at the same time.

This longitudinal field experiment has provided us with various interesting findings. For example, Bossou chimpanzees showed perfect hand preference at the individual level and a weak shift toward using the right hand for stone hammering at the population level. Chimpanzees have also been found to transport not only nuts but also stone tools, demonstrating a rudimentary form of possession of particular stone tools. The infants start using stone tools at around the age of 3.5–5 years old, which also marks the end of a critical period for learning. I applied a syntactical approach using tree-like structure analysis to technical problem solving in tool use behavior. The tool use sequences of chimpanzees range from the simple one-to-one level to hierarchical structures with a variety of nodes: the more nodes in the tree, the more complex the sequence. The action grammar revealed that chimpanzee tool use differs from that of humans in terms of the depth of nodes in the hierarchical structure, especially in the self-embedding recursive structure (Matsuzawa 1996).

A form of observational learning, referred to as "education by master–apprenticeship" (Matsuzawa et al. 2001), plays a key role in the transmission of knowledge and skills from one generation to the next. According to our analysis of observing behavior (Biro et al. 2003), adults are not only the most likely to be the targets of the observation by other members of the group, but also the least likely to be observers themselves. On the other hand, juveniles are rarely targets but often observers, both of adults and of other juveniles. In sum, chimpanzees show a strong tendency to pay attention to the stone tool use of conspecifics in their own age group or older, but not younger. This observation means that cultural innovations are more likely to spread horizontally or vertically/orthogonally downward, but not upward as is sometimes observed in the case of humans.

The learning process underlying the acquisition of nut cracking is characterized by the following three attributes: long-term exposure from birth, high tolerance with no formal instruction from mothers, and intrinsic motivation of infants for imitation not reliant on direct food reward. These features are explored further below.

First, chimpanzee infants are exposed to the nut-cracking activities of others for a long time prior to making their own attempts. Most mothers practice nut-cracking on a daily basis – the skill really represents a tool for survival. Such long-term pre-exposure is likely to be essential for mastering a complex skill, much like long-term exposure to speech sounds precedes production of real speech in human infants.

Second, there is no active teaching, no molding, and no verbal instruction from the mother. However, chimpanzee mothers do show a high tolerance toward their apprentice observers. Infants are allowed to steal nuts from the mothers. I have observed a mother allowing her infant to continuously steal nuts over the course of seven consecutive bouts of cracking. The following two episodes may help to clarify the relationship between master and apprentice. In the first, a 4-year-old infant interrupted the mother's hammering, stole the nut-to-be-cracked from her anvil, and cracked it on her own. In another, a 3-year-old infant picked up a nut from the ground after having watched the mother's nut-cracking for a long time. The infant moved toward the mother and placed the nut on her anvil stone; the mother briefly stopped in mid-motion, then proceeded to crack the nut. The infant removed the kernel from the anvil and ate it.

Third, learning does not depend on direct food reward. As described above, infants can easily obtain kernels from the mother. Moreover, all attempts by infants to manipulate nuts and stones fail to result in even the smallest piece of kernel until the age of 3.5–5 years. In a sense, practicing the manipulating behavior invariably leads to failure and no reward. However, youngsters continue to try their hand at nut-cracking. Motivation thus seems to be intrinsic and drive infants to attempt to produce a copy of the mothers' (or the "masters'") behavior.

Taken together, mother–infant interactions in nut-cracking remind me of the Sushi master–apprentice relationship long established in the Japanese cultural tradition. The master demonstrates as a model in front of the apprentice, but provides no further guidance. The apprentice continues to observe the skill for several years. Such prolonged exposure without formal instruction and/or reward/punishment may be essential for acquiring the complex skill.

In sum, education by master–apprenticeship in chimpanzees is characterized by infants' prolonged exposure to the mother's behavior as a result of a close and long-lasting mother–infant bond, no formal instruction from the mother with neither reward nor punishment, the infants' intrinsic motivation to produce a copy of the mother's behavior, and high levels of tolerance by the mother toward their infants' activities during bouts of observation.

Our study of intelligence in the wild has been focusing on tool-using behaviors and has revealed the importance of social relationships in learning. In other words, learning in wild chimpanzees always occurs within a social context. Infant chimpanzees growing up in a particular community learn the unique cultural traditions of that community from the mother, the father, older siblings, and other members of the group. We have been studying the processes underlying such intra-community transmission by introducing at our outdoor laboratory species of nuts unavailable at Bossou and therefore unfamiliar to the chimpanzees. Such manipulation has allowed us not only to track processes of cultural innovation and subsequent transmission within the group, but also highlight intercommunity transmission (Matsuzawa 1994; Biro et al. 2003).

Extensive survey of Bossou and the neighboring communities revealed that each community of chimpanzees has its unique cultural traditions (Matsuzawa and Yamakoshi 1996; Humle and Matsuzawa 2001). Immigrant females will bring with them the knowledge acquired in their natal community, and through the spread of such knowledge within the group they join, they contribute to the establishment of "cultural zones" in which neighboring communities come to share certain tool-using traditions, while remaining unique in their particular repertoire.

Culture became a central issue in the study of wild chimpanzees in the 1990s (McGrew 1992; Wrangham et al. 1994; Whiten et al. 1999). Questions currently being investigated are exactly when, what, how, and from whom to whom knowledge and skills are passed when they are transmitted from one generation to the next.

From cross-fostering to mother-rearing studies

In the course of the Ai project, we succeeded in performing the first ever artificial insemination of a chimpanzee in Japan. Three babies were born in 1982–83, two of whom were rejected by their biological mother. I thus had an op-

Fig. 5 A classic way of comparing the cognitive development of a chimpanzee infant at 2 months old and a human infant at 9 months old (Photo by T. Mastuzawa, 1984)

portunity to raise a chimpanzee baby at home, and to compare the infant with my own (Fig. 5).

The experience led me to follow the classic study by Ladygina-Kohts (2002), clearly revealing many similarities between the newborns and infants of the two species, humans and chimpanzees. This opportunity resulted in a series of studies of chimpanzee intelligence in face-to-face test situations rather than the automated computer-controlled setting (Matsuzawa 1990b; Myowa-Yamakoshi and Matsuzawa 1999, 2000; Takeshita 2001).

We have learned a great deal about chimpanzee intelligence from ape-language projects and their subjects: Washoe, Sarah, Lana, Kanzi, Ai, and others. Thanks to hand-rearing studies, we have also learned a lot about the perceptual and motor skills of neonatal chimpanzees for direct comparison with humans (Bard et al. 1992; Myowa 1996). However, the experience of raising infant chimpanzees has taught me another key lesson: the importance of the mother–infant bond. I recognized that comparisons of home-reared chimpanzees and home-reared humans were not fair because these chimpanzees were not being raised by their own parents. I noticed that most of our knowledge of the cognitive development of infant chimpanzees came form artificially-reared chimpanzees isolated from their conspecific community. One must not forget that there are aspects of chimpanzee intelligence that can only be explored among members of their own species.

At that time, in the 1980s, laboratory workers began to pay more attention to social aspects of intelligence. "Ape language" studies were declining, while studies of social cognition were on the rise. A landmark paper of the time addressed the issue of *Theory of mind* in chimpanzees (Premack and Woodruff 1978). For almost 2 years from 1985 to 1987, I suspended my study with the chimpanzee Ai and took a sabbatical leave (Matsuzawa 2003b). Although my choice of a destination was unrestricted, I opted for David Premack's lab in Pennsylvania simply because his study was so entirely different from my own way of automated computer-assisted discrimination tasks using a single subject. Whilst there, I was facing questions for the first time about social aspects of chimpanzee intelligence in individuals without any special training of discrimination skills. Around the same time, Premack and Woodruff's work was inspiring a multitude of studies on understanding others' minds, imitation, joint attention, social reference, gaze monitoring, and so forth (Povinelli et al. 1990, Tomasello et al. 1993a; 1993b). In my personal case, I left the issue of social cognition in the laboratory unaddressed, and instead proceeded directly to the wild in 1986 in order to learn more about the chimpanzees' behavior in their natural habitat.

Through my observations and field experiments in Africa, and through my experience of rearing infant chimpanzees in captivity, I came to truly recognize the importance of the community in which an infant chimpanzee grows up and acquires the skills and knowledge unique to the group.

Simulating a community as a whole

Thus we began a laboratory simulation of social intelligence among a group of chimpanzees in KUPRI. The topics we wished to address included observational learning, imitation, deception, and teaching among the members of the community (Tonooka et al. 1997; Matsuzawa 1999; Myowa-Yamakoshi and Matsuzawa 1999, 2000; Hirata and Morimura 2000; Hirata and Matsuzawa 2001).

First, we devoted a considerable amount of effort to modifying the physical environment of our captive chimpanzees in terms of animal welfare and environmental enrichment: we planted about 500 trees belonging to about 60 species in an outdoor compound measuring 700m^2, built 15-m high climbing frames, created a small stream, and built an outdoor booth connected to the main building through underground tunnel (Ochiai and Matsuzawa 1997; Matsuzawa 1999). Then, we performed further rounds of

Fig. 6 The outdoor compound for the group of 15 chimpanzees in KUPRI (Photo by T. Matsuzawa)

Fig. 7 A new paradigm for studying the cognitive development of chimpanzees based on a triadic relationship among chimpanzee mother, chimpanzee infant, and human tester (Photo by Mainichi Newspaper)

Fig. 8 The chimpanzee Ai and her infant Ayumu at 2 years and 4 months. Both are engaged in their own computer task inside a testing booth (Photo by Mainichi Newspaper)

artificial insemination in addition to natural copulation and were rewarded by the arrival of three babies in the year 2000. The KUPRI group has thus grown, and at present comprises a community of 15 chimpanzees of three generations, ranging in age from 0 to 37 years old, and living together in an outdoor compound (Fig. 6).

Bearing in mind the lessons learned from both field and laboratory work, we devised a new paradigm for studying cognitive development in chimpanzees (Matsuzawa 2002; Okamoto et al. 2002; Hayashi and Matsuzawa 2003; Myowa-Yamakoshi et al. 2003). The research method can be described as a sort of "participant observation". The researchers are heavily involved in the daily lives of the chimpanzees by interacting with them directly in their own space. The new paradigm is based on a triadic relationship between a mother chimpanzee, an infant chimpanzee, and a human tester. The experiments take place in a large booth, which the experimenter enters with both the mother and her infant already inside (Fig. 7). As the mother looks on, the tester presents the infant with a variety of tasks, and provides social reinforcement. In this way, the close bond established between the human experimenter and the mother – based on years of experience and daily interaction – allows us to test the infant chimpanzees in much the same context as that in which human infant developmental tests are conducted. In a face-to-face situation and with the mothers' cooperation, we are able to closely replicate many such tests, as well as design our own for illuminating developmental changes in the chimpanzee infants. We have been following the infants' development in object manipulation, the use of tools, drawing skills, the recognition of faces, facial gesture imitation, mirror self-recognition, the understanding of gaze and pointing as referents, and so forth.

The final issue I would like to address here concerns cultural transmission of chimpanzees' knowledge and skills from one generation to the next. When, from whom to whom, and how are knowledge and skills passed on? Outside our new paradigm of "chimpanzee mother–chimpanzee infant–human tester triad", the chimpanzees themselves have begun to transfer skills in computer-controlled tasks within a closed space without any help from or interaction with humans (Fig. 8). In one such situation, all three infant chimpanzees mastered the skill of using honey fishing tools at the age of 1 year and 10 months, after observing skillful mothers (Hirata and Celli 2003). Not only the infants' own mother but also the other adult females of the community served as models for these infants.

One particular infant, Ai's son, Ayumu, suddenly began to perform matching-to-sample discrimination on the computer screen at the age of 9 months, after having closely observed his mother's behavior from right after birth (Matsuzawa 2002). We can be certain that this learning was not shaped by food reward, since the reward itself was a token (a coin): a piece of metal that could not be eaten. Then, at the age 2 years and 3 months, Ayumu learned how to insert the token into a vending machine – an action for which he did receive a food reward (Sousa et al. 2003). The data gathered in these experiments conducted in a captive community clearly simulate our findings from the wild, and underline the importance and validity of education by master–apprenticeship for socially mediated acquisition of knowledge in chimpanzees.

The Ai project has now entered its third decade, and has progressed from the study of the single individual to a simulation of the chimpanzee community as a whole. I hope that parallel efforts in the laboratory and in the field will help us to broaden our understanding of the similarities and the differences between humans and chimpanzees.

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