Anim Cogn (2009) 12 (Suppl 1):S1–S9
DOI 10.1007/s10071-009-0277-1

REVIEW

# The chimpanzee mind: in search of the evolutionary roots of the human mind

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Received: 25 September 2008 / Revised: 3 August 2009 / Accepted: 4 August 2009 / Published online: 29 August 2009


**Abstract** The year 2008 marks the 60th anniversary of Japanese primatology. Kinji Imanishi (1902–1992) first visited Koshima island in 1948 to study wild Japanese monkeys, and to explore the evolutionary origins of human society. This year is also the 30th anniversary of the Ai project: the chimpanzee Ai first touched the keyboard connected to a computer system in 1978. This paper summarizes the historical background of the Ai project, whose principal aim is to understand the evolutionary origins of the human mind. The present paper also aims to present a theoretical framework for the discipline called comparative cognitive science (CCS). CCS is characterized by the collective efforts of researchers employing a variety of methods, together taking a holistic approach to understand the minds of nonhuman animals. While the researchers of animals usually carry out experiments in the laboratory and conduct observational studies in the natural habitat, a different permutation is also possible. Field experiments can be carried out in the natural habitat, and observational studies can be in the laboratory. Such a two-by-two contingency table based on location and research method thus provides the basis for a holistic approach. CCS provides a unique window on understanding the chimpanzee mind as a whole. The studies of the chimpanzee mind may also result in illuminating the evolutionary roots of the human mind.

This contribution represents the introduction to the Supplement Issue "The Chimpanzee Mind".

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**Keywords** Chimpanzee · Psychophysics · Comparative cognitive science · Field experiment · Participation observation · Ai project

## Sixty years of Japanese primatology and the Ai project

The year 2008 is the 60th anniversary of the birth of Japanese primatology. Kinji Imanishi (1902–1992) first arrived on Koshima island to study Japanese monkeys in the wild on 3 December 1948 (Matsuzawa and McGrew 2008). Imanishi and his colleagues were interested in the evolutionary origins of human society. They thus decided to study monkey societies, exploring various aspects of ecology and behavior: dominance rank, breeding season, solitary males, matrilineal lineage, vocal communication, and cultural traditions such as sweet-potato washing (Hirata et al. 2001; Matsuzawa 2002). Sixty years later, researchers from Kyoto University still continue the long-term observation of the wild monkeys on Koshima (Fig. 1)—they have so far recorded the history of eight generations. Thanks to the efforts of Imanishi and his colleagues in Japan and later in Africa, the Japanese government founded the Primate Research Institute of Kyoto University (KUPRI) in 1967. To the present day, KUPRI continues to be an international center of primatology in various domains.

I got into Kyoto University in 1969 when I was 18 years old and there was no entrance examination in the University of Tokyo because of the world-wide student power fights against authorities (Matsuzawa 2009a). I was in Kyoto University but had no interest at all in primatology during my time there. Following Kyoto University's long tradition in outdoor pursuits, I became a member of the Academic Alpine Club of Kyoto (AACK). The club was founded in 1931 (also by Imanishi and his colleagues) with the aim of climbing K2, the second highest mountain in the

**Fig. 1** Sweet-potato washing by a Japanese monkey on Koshima island (photo by Tetsuro Matsuzawa)

world, yet to be conquered at the time. Thus, in my early career, I was a Himalayan mountaineer. I joined the AACK expedition to one of the virgin peaks of Mount Kangchenjunga, whose highest peak at 8,598 m makes it the third highest mountain in the world. I went there twice, first at the age of 22 in 1973, then at the age of 33 in 1984. I made it to 8,250 m in Kangchenjunga without oxygen, but failed to reach the summit (Fig. 2). However, the failures led me to successfully reach the summit of Muztagh Ata (7,546 m) in Xinjiang in 1989, and to the summit of Xixabangam (8,027 m) in Tibet in 1990. I learned a lot from mountaineering about the importance of planning, execution, and monitoring myself. What I learned was the pioneering spirits and the importance of logistics to reach to a goal.

My major, as an undergraduate, was philosophy. However, I did not feel I was getting much satisfaction simply from reading books written by distinguished philosophers of the past. Searching for a subject that interested me more, I became an experimental psychologist, focusing on human visual perception. The first study that I was truly fascinated by was the work of Julez (1971) on binocular depth perception using random dot stereograms. While when viewed monocularly the stimuli appeared no more than random black and white dot patterns, binocular vision gave subjects clear depth information. I was also fascinated by the McCollough effect (McCollough 1965), a contingent color after-effect dependent on the orientation of white–black grating patterns. In both cases, humans experience psychological phenomena that cannot be explained by the properties of the physical world alone. Nevertheless, through the study of visual perception, I recognized that the eyes were simply a window to the outer world. It is not the eyes but the brain that really perceives and interprets this world.

**Fig. 2** A self-portrait on Kangchenjunga, 1984

My research interest shifted from wanting to understand why we have two eyes to why we have two brain hemispheres. This happened to coincide with Sperry and Gazzaniga's studies with a split-brain patient, and their discoveries of the functional asymmetry of the left–right hemispheres (Gazzaniga 1970; Sperry 1974). My graduate supervisor was the late Toshitsugu Hirano (1930–1993). In turn, his supervisor in the United States had been James Olds (1922–1976), who originally identified the "pleasure center" of the brain, showing that electric stimulation in the hypothalamus of rats could serve as a reward system (Olds and Milner 1954). Under the supervision of Hirano, I began to study the reversible split-brain in rats using the technique of cortical spreading depression, putting potassium crystals on the brain surface to suppress the activity of one hemisphere and keep the other intact (Bures et al. 1974). I then shifted to a major in physiological psychology, studying memory traces in rats. Drawing together human visual perception and rat behavior analysis, I became interested in the study of the visual world of nonhuman animals by controlling and examining their behavior.

In 1976, at the age of 26, I was appointed associate professor at the Department of Psychology at KUPRI. I became interested in animal psychophysics—an approach in which researchers attempted to understand the perception of nonhuman animals through operant techniques (Blough 1955; Humphrey 1971; Stebbins 1970). My first study at the institute examined visual unisotropy of orientation detection in Japanese monkeys. Monkeys were sensitive to slight changes in the orientation of black and white stripes when these were presented vertically or horizontally. However, they were not sensitive to such changes in orientation when the stripes were aligned orthogonally—precisely the same phenomenon had been identified in humans. A year after I began at KUPRI, a chimpanzee named Ai arrived at the institute. It was Professor Kiyoko Murofushi (1927–) who planned to initiate an Ape language study in Japan in the late 1970s, and set up the project with the intention that Ai would be its principal subject.

I joined the project, and Professor Murofushi allowed me to do whatever I wished—as long as the study was in some way related to human language.

## The Ai project: understanding the perceptual world of chimpanzees

The year 2008 marks the 30th anniversary of the Ai project. The chimpanzee Ai first touched a keyboard connected to a computer system on 15 April 1978. Since then, my colleagues and I have been working towards understanding the evolutionary origins of the human mind. Our approach entails the study of the chimpanzee mind, seeking to uncover similarities and differences between humans and their closest evolutionary relatives. The scientific achievements of the Ai project have been published in many articles, and have also been collated in two books published by Springer (Matsuzawa 2001; Matsuzawa et al. 2006).

The very first day I met Ai remains vivid in my memory. It was a chilly day in November 1977. I went down to a room in the basement of the institute. There were no windows and no light except a bulb hanging from the ceiling. A tiny chimpanzee was sitting on a bench. I looked into her eyes. She looked back into mine. We held each other's gaze, and what surprised me most was that she showed signs neither of fear nor of threat. In my experience with monkeys, I had learned that a direct gaze had clear aggressive connotations—a Japanese monkey would, in response, open his mouth in an attempt to threaten, or retract his lips and reveal his teeth, in a grimace that signals fear of a stranger. However, this infant chimpanzee continued to look into my eyes. I had nothing with me; no gift to the tiny newcomer. Then, I noticed that I happened to be wearing arm warmers over my lab coat. I took off one arm warmer and showed it to her. She received it and paused for a while. Then, she suddenly pulled it up over her arm, and played with it for a while, moving it up and down along her arm. Eventually, she extended her arm and gave me back the arm warmer. I took it. All the while, she continued to look into my eyes. At that moment, she touched my heart, and I touched her future (Fig. 3).


**Fig. 3** Ai at the age of 4 (in 1981)

When we began the Ai project, there had already existed three pioneering programs of so-called ape language study initiated by psychologists in the West: the Gardners' efforts with the chimpanzee Washoe using American sign language (Gardner and Gardner 1969), the Premacks' work with the chimpanzee Sarah using plastic sign language (Premack 1971), and the Rumbaugh's studies with the chimpanzee Lana using Yerkish lexigrams (Rumbaugh 1977). Although we had no experience with these kinds of ape studies, by the mid-1970s the researchers of KUPRI had already accumulated extensive knowledge on controlling the behavior of nonhuman primates with the help of computer-based equipment and operant conditioning (Matsuzawa 2003). Therefore, we decided to use a computerized system to analyze chimpanzee behavior.

However, questions along the lines of "Can apes acquire human language?" seemed too vague to me. I was interested in the perceptual world, neither in communication nor language itself. Therefore, I decided to teach chimpanzees language-like skills only as a medium to gain access to their mind. I did not care whether the skills themselves qualified as language or not: I wanted to learn what chimpanzees saw, what they knew, what they thought, etc., all through a sound, scientific method. I tried to gain access to the perceptual world of Ai with the help of symbolic media such as numerals, lexigrams, Kanji characters, and letters of the alphabet.

Thus, what the Ai project originally set out to do was to uncover the perceptual world of chimpanzees, in other words, to establish the psychophysical analysis of the mind. Ai was the first chimpanzee who learned to use Arabic numerals to represent number (Matsuzawa 1985a, 2009b). She learned lexigrams—specially developed visual symbols—corresponding to 11 color names. Her color classification of hundreds of Munsell color chips told us that humans and chimpanzees have many similarities in their color perception and classification (Matsuzawa 1985b). Ai learned letters of the alphabet to represent various humans and chimpanzees she was familiar with (Matsuzawa 1990). She showed a clear species-specific bias in identifying individuals: it was easier for Ai to identify chimpanzees rather than humans, while human subjects performed better with humans as stimuli when tested on the same task. We also found an important difference between human and chimpanzee perception: pictures of faces presented upside down were usually difficult for human subjects to recognize, but not for Ai, who performed well even on such rotated stimuli (Tomonaga et al. 1993). This result might reflect differences in the two species' ecology: humans, who live terrestrially, are constrained in an upright posture, whereas chimpanzees move more freely in three-dimensional space as part of their arboreal lifestyle.

The Ai project is at the tail-end of ape language studies carried out in the second half of the twentieth century, and a front runner of studies of comparative cognition in chimpanzees. In 2007, the chimpanzee Washoe (Fouts and Mills 1997) passed away, as did Alex the parrot (Pepperberg 2002). These sad events suddenly made me realize that I may have been the only person who had opportunities to meet all of language studies' chattering nonhuman animals. I met Washoe, Sarah, and Lana chimpanzees, and, of course, Ai. I visited Koko the gorilla (Patterson et al. 1981), met the bonobos Kanzi and Panbanisha (Savage-Rumbaugh and Lewin 1994), and the orangutan named Chantek (Miles 1990) at Atlanta Zoo. When I gave a talk at the University of Hawaii, I met the dolphins Akeakami and Phoenix (Herman et al. 1984).

While all these meetings were memorable in their own way, I will never forget the day I came face to face with Alex the parrot, on a windy day in Chicago. I was visiting Irene Pepperberg, based at Northwestern University at the time. The chimpanzee Ai had already succeeded to use Arabic numerals to represent the number, and lexigrams to represent the color and the object name, of sets of items displayed to her—such that she could respond with "red/pencil/five", by touching the corresponding symbols on a keyboard, when she was shown five red pencils (Matsuzawa 1985a). However, Alex the parrot described, in *spoken* English, the five red pegs shown to him by Irene—and his English pronunciation was much better than mine! It thus became clear that nonhuman animals can, to some extent, learn language-like skills to inform us about how they represent this world. However, it also emerged that there were constraints in their representational capability (Terrace et al. 1979). While they can master the level of icons or words, there are no examples of subjects learning more than 1,000 "words". Crucially, there is also very little evidence of syntactic structure, of combining words to create new meaning in a way ubiquitous in human language.

## Field study in Africa

In February 1986, I went to Africa for the first time. I was already aware of chimpanzees' impressive levels of intelligence through my days with Ai and the other chimpanzees at KUPRI. Then, a naïve question came to my mind: How is chimpanzee intelligence utilized in the natural habitat? After 8 years focusing on Ai chimpanzee and her cognitive tasks, I took sabbatical leave, which I spent at David Premack's laboratory at the University of Pennsylvania. At the time, Premack was researching the existence of a "theory of mind" in chimpanzees, together with some other related topics (Premack and Woodruff 1978; Premack 1985). Besides conducting face-to-face tests with their captive chimpanzees (including Sarah chimpanzee), I also took up an opportunity to go to Africa for the first time in my life. I visited Bossou, Guinea, West Africa, where my KUPRI colleague, Yukimaru Sugiyama, had begun his study of wild chimpanzees. I was the second researcher to visit the Bossou site. I still remember the very first day I saw wild chimpanzees in the forest. They moved from one tree to the next right in front of me. The hair covering their bodies was the deepest black, shining in the early morning sun, and we were surrounded by a gentle breeze and the soft sound of leaves. Unfortunately, Sugiyama developed symptoms of malaria the next day after I arrived. I looked after him for a few days, then the decision was made that he should return to Japan. I was left alone in a small and remote village in Africa, where I spent the next 2 months.

After returning from Africa, I attended the first "Understanding Chimpanzees" meeting in Chicago in November 1986, where I met Jane Goodall for the first time. The meeting was to celebrate the publication of her landmark book (Goodall 1986). This opportunity provided me with food for thought regarding some of the pioneering efforts in the study of chimpanzees, as well as about my own plans for the future. Premack had already done an excellent study of chimpanzee intelligence in the laboratory. Goodall had already conducted her groundbreaking field work in Africa. I was just a young scientist who had begun a study of the chimpanzee mind. What was I to do next? The experience and knowledge I gained during my mountain-climbing days in the Himalayas gave me the inspiration about where to look for the first ascent in the academic world. My answer was to make parallel efforts in the laboratory and in the field. I had two mentors, David Premack and Jane Goodall. David is a great scholar but does not do field work, and Jane will not carry out experiments in the laboratory. I had found a simple solution: my aim became the synthesis of laboratory and field work.

Over the past 23 years, I visited Bossou at least once a year to carry out fieldwork. My research target was tool use, with a particular focus on the use of stone tools to crack open nuts (Matsuzawa 1994). Bossou chimpanzees use a pair of mobile stones as hammer and anvil to crack open oil-palm nuts (Fig. 4). While nut-cracking itself is restricted to chimpanzee communities in the western part of Africa, the use of mobile hammer and anvil stones is a unique cultural tradition of the Bossou community (Biro

**Fig. 4** Stone tool use by Bossou chimpanzees (photo by Etsuko Nogami)

**Fig. 5** Facial imitation experiment with an infant chimpanzee (photo by Nancy Enslin)

et al. 2003). For detailed analysis of the behavior, we invented a "Field experiment": we provided a set of stones and nuts to wild chimpanzees at a fixed location within the forest, where we were able to observe and video record their behavior from close range and at reliable intervals over many consecutive years. This brought to light several new and interesting findings: perfect laterality in hand use, a critical period for learning the skill, the possession and transportation of tools and nuts, and a putative model of the learning process, referred to as "Education by master-apprenticeship" (Matsuzawa et al. 2001), among others.

Fieldwork has also helped to shed light on the life history of chimpanzees (Emery-Thompson et al. 2007). The lifespan of wild chimpanzees is about 50 years. The inter-birth interval is about 5 years. During the first 5 years, the infant monopolizes the mother; there are no siblings separated by only 2 or 3 years, yet this is a popular age gap in human societies. The chimpanzee mother–infant relationship is characterized by the rearing of a single offspring at any one time by the mother only—a situation resembling the case of the single working mother. On the contrary, the human mother–infant relationship is characterized by the rearing of multiple children simultaneously, with the assistance of multiple care takers. Children are looked after not only by the mother but also by the father, grandparents, aunts, and helpers, in many cases aided even by a wide network of community support.

## Participation observation

In the year 2000, the Ai project entered a new phase: Ai gave birth to a son named Ayumu on 24 April. Besides Ai, two other female chimpanzees gave birth at KUPRI in 2000. All three infants were reared by their biological mothers. Thanks to the long-term relationship between researchers and the chimpanzee mothers, we were able to ask for the mothers' help in examining many aspects of their infants' cognitive development. We called our novel approach "Participation observation", in which the trio of chimpanzee infant, mother, and researcher all worked together based on triadic friendship (Fig. 5).

The new method brought forth many new findings, such as the existence of neonatal smiling in infant chimpanzees, neonatal facial imitation, special preference for direct gaze, discrimination of the mothers' face, etc., all these were features shared with humans (Myowa-Yamakoshi et al. 2004; Tomonaga et al. 2004). The face-to-face test clearly demonstrated the similarity and the difference between the two species in the physical-causal recognition of objects (Hayashi 2007a, b; Hayashi and Matsuzawa 2003). The study also revealed clear differences between humans and chimpanzees in various developmental aspects, such as the mother–infant relationship. Many people believe that bipedal upright posture and bipedal locomotion are among the most important and unique characteristics of humans. According to the bipedalism hypothesis, the upright posture made the freeing of the hands that facilitated the manipulation of objects and made tool use possible. However, our participation observation clearly showed an alternative explanation, the "supine posture hypothesis": physical separation of mother and infant, and the infant's ability to assume a stable supine posture from right after birth (Matsuzawa 2007; Takeshita et al. 2009).

Chimpanzee infants, as well as orangutan infants, cannot assume a stable supine posture when they are laid on their back. They slowly lift up one arm and the contralateral leg, then a few seconds later, they switch both arms and legs and lift those on the opposite side. The alternation in limb movement suggests that this is not a stable posture for them—ape infants need to cling to the mother. For at least the first 3 months of their lives, they are never separated from the mother. In contrast, human infants are physically separated

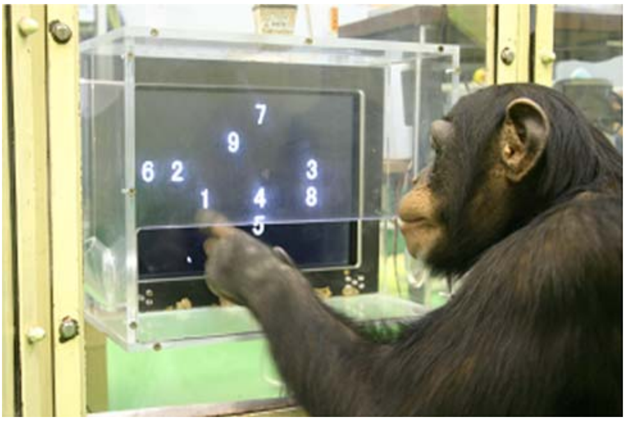


**Fig. 6** Ayumu, the young male, working on the numerical sequence task (photo by Tetsuro Matsuzawa)

from their mother from the very first day—this, together with a stable supine posture, leads to a great deal of face-to-face communication, including looking into each other's eyes, smiling, waving, and vocal exchange. Chimpanzee infants never cry at night: they have no need to do so as they are constantly embraced by the mother. Human infants, on the other hand, are often physically separated from the mother during both day and night, and receive a lot of allomothering behavior from family members. Perhaps less well appreciated is the importance of the supine posture in terms of tool use. When supine, an individual's hands are free from clinging. Although bipedalism starts at around 1 year of age, it is the stable supine posture from right after birth that makes hands free and facilitates a much earlier onset of object manipulation in a uniquely human fashion.

KUPRI's three chimpanzee infants—Ayumu, Cleo, and Pal—have revealed many different aspects of chimpanzee cognition and development over the past 8 years. For example, after they learned the order of the numerals 1 through 9 (Fig. 6), we were able to test their memory capacity in direct comparison with humans. In a "photographic memory" task, the young chimpanzees outperformed human adults (Inoue and Matsuzawa 2007). Previous studies had already proved that the memory of Ai chimpanzee was somehow comparable to human adults (Biro and Matsuzawa 1999; Fujita and Matsuzawa 1990; Kawai and Matsuzawa 2000). However, the young chimpanzees' performance clearly showed us that chimpanzees can be better than humans in a cognitive task. Even after long extensive training of graduate students, no one can remember 9 numerals at a glance and start touching the first one in 0.6 s.

## The perspective of comparative cognitive science (CCS)

The year 2008 is also the 30th anniversary of Premack and Woodruff's landmark article on Theory of Mind (Premack and Woodruff 1978). This paper inspired many researchers to begin studying social aspects of intelligence. Each animal species lives in its own unique world, called "Umwelt" by Jakob von Uexküll (1864–1944), and their cognitive skills are honed accordingly (von Uexküll 1909). For example, some birds display extraordinary memory skills when remembering the location of cached food (Clayton and Dickinson 1998), while others possess impressive abilities to navigate over long distances (Biro et al. 2007). Primates have evolved a high degree of social intelligence due to their extremely rich and complex social lives (Jolly 1966; Herrman et al. 2007; Humphrey 1976; Byrne and Whiten 1988; de Waal 1988). Social intelligence has emerged as one of the central topics in studies of primate cognition (Tomasello and Call 1997; Hare et al. 2000; Whiten 2000; Call 2001).

However, is it valid to maintain a dichotomy between social intelligence and physical intelligence? For example, let us look at the development of stone tool use in chimpanzees. Chimpanzees in Bossou start to utilize stone tools at the age of 3–5 years. There are various developmental stages that young chimpanzees go through on their way to acquiring the skill (Inoue-Nakamura and Matsuzawa 1997). They start by manipulating a single object at a time: holding a nut, rolling a stone, etc. They then start manipulating objects sequentially, or manipulating multiple objects simultaneously. Finally, they combine all the actions in the correct order. All the while, infants spend long periods carefully observing the behavior of older members of the community (Biro et al. 2003). Social intelligence and material intelligence can therefore not be separated—they are highly interconnected. In fact, both are involved in the acquisition of tool use. It is no more valid to maintain a dichotomy between social intelligence and physical intelligence. We have called this kind of socio-material behavior shown during the acquisition process "Education by master-apprenticeship" (Matsuzawa et al. 2001). This form of "education" is characterized by observational learning, in turn facilitated by the long-term mother–infant bond, no active teaching by the mother, a strong intrinsic motivation by the infant to produce a copy of the mother's behavior, and a high tolerance of the mother toward the infant during bouts of observation.

The umbrella term under which we view our current efforts is a discipline referred to as CCS (see Matsuzawa and Tomonaga 2001). Cognitive science is the scientific study of the human mind. The comparison of different species represents a royal road to understand the essential parts of phenomena, as in the case of comparative anatomy, comparative physiology, comparative genomics, etc. Therefore, CCS can be defined as the study of the human mind and its evolutionary origins, through comparisons of different species. The CCS of humans and chimpanzees is the focus of

**Table 1** The two-by-two matrix of methods employed in comparative cognitive science

| Location | Method | |
|---|---|---|
| | Experiment | Observation |
| Laboratory | Laboratory experiment | Participation observation |
| Natural habitat | Field experiment | Field observation |

this special issue. It covers many parallel strands of our work, from laboratory experiments to observations in the natural habitat, and from field experiments to participation observation in the laboratory. These in fact constitute a two-by-two matrix of approaches to exploring cognition: experiment versus observation and laboratory versus the natural habitat (Table 1). Taken together, CCS can now draw on 30 years of the Ai project, as well as continue attempts to understand the chimpanzee mind as a whole and to uncover the evolutionary origins of human mind.

This special issue highlights recent progress in our studies of chimpanzees from a CCS perspective. In the present volume, we have included *laboratory experiments*: working memory (Inoue and Matsuzawa 2009), cross-modal recognition (Martinez and Matsuzawa 2009), visuo-spatial attention (Tomonaga and Imura 2009); *field observations*: tool composite use and reuse (Carvalho et al. 2009), social influence on the acquisition of tool use (Humle et al. 2009); *face-to-face tests in the laboratory*: stacking irregularly shaped blocks (Hayashi and Takeshita 2009); *field experiments on tool use among wild chimpanzees* (Sousa et al. 2009). Some are single subject studies, while others rely on multiple subjects and focus on social aspects of intelligence in tool-using contexts: stone tool use acquired in a group (Hirata et al. 2009); token transfer between mother and offspring (Tanaka and Yamamoto 2009); selfish tactics versus reciprocal cooperation (Yamamoto and Tanaka 2009). Drawing together these different strands of our research, we are trying to approach the chimpanzee mind as a whole.

From a comparative perspective, CCS of humans and chimpanzees provides the most important contribution to our attempts to gain insight into the mind of our ancestors 5–7 million years ago. My hope is that this special issue will become another window onto the evolutionary origins of human cognition, and onto the minds of nonhuman animals.

I would like to express my sincere gratitude to the editor of Animal Cognition, Tatiana Czeschlik. She long ago recognized the importance of our chimpanzee research, and her continuous support over many years encouraged us to continue our work towards understanding various aspects of the chimpanzee mind. Upon the 30th anniversary of the Ai project, she provided us with the opportunity to assemble papers representing all four approaches in our matrix of methodologies aimed at understanding the chimpanzee mind. As you will see in the table of contents, the authors are not limited to Japanese researchers, but also include many foreign collaborators—particularly in our field studies at Bossou and Nimba. I hope readers will enjoy becoming acquainted with the various studies of the chimpanzee mind contained within, and will reflect on how these might help us to clarify the evolutionary roots of the human mind. I also hope our scientific activity will help to promote conservation efforts in the wild as well as welfare in captivity for chimpanzees, our evolutionary neighbors.

**Acknowledgments** The study was financially supported by MEXT grant # 20002001 and JSPS-HOPE/ITP-HOPE to the author, and JSPS global COE program (A06, biodiversity). Thanks to my colleagues and students at the Primate Research Institute of Kyoto University, especially Drs. Masaki Tomonaga and Misato Hayashi. Special thanks to Dr. Dora Biro of Oxford University for her careful reading of the manuscript.

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