Evolution of the brain and social behavior in chimpanzees
Tetsuro Matsuzawa

The comparison of humans and chimpanzees is a unique way to highlight the evolutionary origins of human nature. This paper summarizes the most recent advances in the study of chimpanzee brains, cognition, and behavior. It covers the topics such as eye-tracking study, helping behavior, prefrontal WM volume increase during infancy, and fetal brain development. Based on the facts, the paper proposed the “social brain hypothesis.” Chimpanzees are good at capturing images as a whole, while humans are better at understanding the meaning of what they see. Chimpanzees apparently focus on the salient objects, neglecting the social context. In contrast, humans always recognize things within the social context, paying preferential attention to people, as agents. This is consistent with the fact that humans are highly altruistic and collaborative from a very young age. Thus, humans have evolved towards increased collaboration and mutual support. This kind of evolutionary pressure may have provided the basis for the development of the human brain with its unique functions.

Address
Primate Research Institute, Kyoto University, Japan

Corresponding author: Matsuzawa, Tetsuro (matsuzawa@pri.kyoto-u.ac.jp)

Cognitive development in chimpanzees
This paper aims to summarize the most recent advances in the study of chimpanzee brains, cognition, and behavior. The comparison of humans and chimpanzees provides a unique opportunity to highlight the evolutionary origins of human nature. The first section addresses cognitive development. We have conducted a series of studies on comparative cognitive development in humans and chimpanzees both in the wild and in the laboratory [1,2]. The methodology used [1,2] in the laboratory is called participant observation, whose unique aspect, in contrast to previous ape-language studies, is that infants are not separated from their mothers. The approach instead has infants raised by their biological mothers, and nurtures a long-standing rapport between these chimpanzee mothers and the researchers. This has allowed us to test the cognitive development of infants in an intimate face-to-face situation, in the presence and with the tolerance of the chimpanzee mother. Recent advances have been made in this line of research in elucidating a wide variety of processes including: visual illusions [3], movement and depth perception [4,5], face recognition [6], gaze detection [7], social cueing [8–10], contagious yawning [11], self-awareness [12], object manipulation [13], tool use [14,15], cooperation [16], and others.

The most striking difference reported to date between the two species is a remarkable ability to use visual working memory in young chimpanzees, who can outperform even adult humans on certain tasks [17–19] (Figure 1).

Specifically, chimpanzees can learn to touch the Arabic numerals, 1–9, in ascending order. Once trained to criterion on this task, we introduced a masking task to measure working memory ability. Upon touching the lowest number, the remaining eight numbers are masked by white squares and subjects are then required to touch the masked stimuli in ascending order of the hidden numerals. This is not an easy task for humans; however, three out of three young chimpanzees succeeded. The young chimpanzees performed better in terms of speed and accuracy than both their own mothers and human adults. Ayumu, the most skilled participant, can do the task with nine numerals at 5.5-year-old, with a latency of 0.67 seconds to touch the first number ‘1’ and a level of accuracy above 80% [17]. This cannot be achieved by human subjects even if they are trained for an extended period.

Chimpanzees also learned two versions of the matching-to-sample (MTS) task: either an identity task, or a symbolic task [19]. In an example identity MTS task, the sample is the color red and the alternative response choices the color red versus the color green. Touching the matching color, red, is the correct choice. In the symbolic MTS task, the sample is a color, for example red, and the alternative responses are symbols, representing the matching color, red, and a different symbol representing a non-matching color (e.g. green). Touching the symbol corresponding to the sample color, in this case red, is the correct choice.

Chimpanzees can learn the identity MTS task, but have difficulty with the symbolic MTS task. Continuous training allowed the chimpanzees to master the task of choosing the symbol corresponding to the sample color. A reversed-order task can then be introduced, that is, presenting a
2 Social & emotional neuroscience

Figure 1

Visual working memory in chimpanzees. Chimpanzee Ayumu is doing the masking task of memorizing nine numerals at a glance. Photo taken by T. Matsuzawa.

symbol as the sample, and colors as the alternative responses. This reversed task is easy for humans, but appears not to be so for chimpanzees [19]. This finding was replicated in a recent study of collaborative MTS in which two chimpanzees were required to collaborate on the task [20].

These findings support the interpretation that chimpanzee cognition is characterized by quickly grasping the whole image, somewhat like capturing an image with a camera (eidetic or photographic memory), while human cognition is better characterized by seeing things while understanding the associated meaning.

Eye-tracking studies in chimpanzees

This human tendency to see things within context and meaning has also received support from a recent series of studies by Kano and Tomonaga using eye-tracking with a range of ape species (chimpanzees, gorillas, orangutans) [21–23]. The subject sits in front of the monitor screen, with an eye-tracker located below. Stimuli, either a still picture or a video clip, are then displayed on-screen. These studies found that both humans and chimpanzees preferred to look at the face in comparison to other parts of the body. However, though the total time allocation was the same, the fixation pattern was different. Fixation in Chimpanzees moved quickly from one place to another with large amplitude saccades, for example, from eye to foot to eye to shoulder. Human spontaneous gaze shift instead changes more smoothly, for example, moving from eye to nose, to mouth, to chin [23].

One qualitative way to describe the difference between the fixation pattern in humans and chimpanzees comes from a study in which stimuli were a mixture of face and non-face pictures presented briefly in alternating succession. Chimpanzees spontaneously and rapidly followed the contents of each picture with their gaze, whereas human gaze tended to stick on the face stimuli. Humans have a strong spontaneous tendency to fixate longer on faces compared to other stimuli [21].

A recent eye-tracking study clearly demonstrated the importance of social context to human infants [24*]. The subjects, chimpanzees and one-year-old human babies sat in front of the monitor in the presence of their caretaker or mother. The stimulus presented was a video clip showing a young woman holding a bottle of juice and pouring it into a glass. Chimpanzees watched the bottle and the glass and did not attend preferentially to the woman. In contrast, human infants’ gaze shifted back and forth between the woman’s face, the bottle and the glass. Humans appear to see target events within a social context, always paying preferential attention to the person (Figure 2).

Taken together, the studies reviewed thus far suggest that humans have a tendency to focus on the meaning of what they see, and also to see things within a social context.

Altruistic behavior

Chimpanzees in the wild show a highly developed tool technology [25] and also altruistic behavior [26–29]. Altruistic behavior has also been investigated in the laboratory [30]. Yamamoto and Tanaka carried out a series of experiments in which two chimpanzees faced a collaborative task [31,32,33–35]. Most striking was the lack of reciprocity in chimpanzees, consistent with field observations of chimpanzee interaction [1]. Chimpanzees in the wild behave altruistically, for example, a mother chimpanzee helps or shares food with her offspring. However, the reverse is not true; the infant chimpanzee never gives food to his/her mother. In contrast, altruistic behavior emerges at a very early phase in human development.

Mutual help is referred to as reciprocity. Reciprocal altruism was not found in chimpanzees. For example, in one study, chimpanzee A is in one room while another, chimpanzee B, is next door. Chimpanzee A can insert a token into a vending machine that then delivers food to chimpanzee B. At the same time, conversely, chimpanzee B can insert a token resulting in the output of food to chimpanzee A. The two chimpanzees were given 500 tokens each, simultaneously. Suppose that this was done with human subjects — we would surely expect them to collaborate by inserting the tokens for delivering food for their neighbor reciprocally. The chimpanzees, however, did not insert any tokens and so both failed to get a food reward [33].
A recent study revealed an interesting aspect of chimpanzee collaboration: helping behavior on demand. Chimpanzee A had a set of tools such as sticks, straw, rope, etc. Chimpanzee B, in a room next-door, was presented with a foraging task to solve, for example, a bottle of juice was placed out of reach so that chimpanzee B needed a stick to retrieve it. In another example, a tiny hole in the wall allowed chimpanzee B to access a bottle of juice with a straw, if she has one. Thus, chimpanzee A had the tool-set required for solving the problems presented to chimpanzee B. The results showed that chimpanzee A did not spontaneously help chimpanzee B. However, when chimpanzee B extended and waved a hand through a window between the adjacent rooms (in request) chimpanzee A gave the necessary tool to chimpanzee B. It must be noted that chimpanzee A handed the correct tool for the task, for example, a stick for retrieving the out-of-reach bottle. This strongly suggests that chimpanzee A understood why chimpanzee B was in need [30,32] (Figure 3).

Suppose that this was done with human subjects — they would be likely to spontaneously give the right tool to their neighbor, even in the absence of any explicit request from the person in difficulty. In chimpanzees, altruistic behavior was not evident until it was clearly requested. Taken together, humans show spontaneous altruistic behavior without requests, and also display reciprocal altruism. These results indicate that mutual support in a social context may be uniquely human.

There are good amount of empirical studies reporting a New World monkey species, capuchin monkeys (Cebus Apella), also show altruistic behavior (for review: [36]). There are, however, very few systematic studies on the altruistic behavior in the other apes and monkeys. There are some anecdotes in captive bonobos about the human-like spontaneous altruistic behavior. The apes raised by humans in the human environment can show many human-specific behavior including altruistic behavior. However, the reciprocal altruism is not yet reported. Suppose that there is a human mother with her young child at the age of two years sitting in front of a plate of strawberries. Mother may pick up a piece and give it to her child. Then, the child may put a piece into the mouth of the mother. This kind of behavior is ubiquitous in humans but not in the other species.

Brain function and development in chimpanzees

Human brains increased dramatically in size after the emergence of the genus Homo. The size of the cerebrum,
in particular, is much larger in humans than in other primate species. While it is possible to estimate total brain volume from cranial capacity, fossil records do not provide more detailed information than that, because the brain itself cannot, of course, be preserved in fossils.

Chimpanzees are the closest living relatives of humans and give us the only opportunity to examine real brains closely related to our own. A recent trend in cognitive studies on chimpanzees has been a focus on uncovering the neural correlates of behavior using noninvasive techniques, just as with human subjects. Hirata and colleagues were the first to successfully record an EEG from an awake chimpanzee using a completely noninvasive technique, similar to that used for humans [37,38]. The chimpanzee quietly sat in a chair and allowed the experimenter to put electrode patches on the skin of her forehead, top of the head, etc. (Figure 4).

The EEG and ERP studies showed clearly that the chimpanzee was able to recognize her own name: ‘Mizuki’ [39,40]. Previous behavioral studies supported this kind of auditory comprehension in chimpanzees to some extent. Moreover, chimpanzees may have visual-auditory integration, just like humans [41,42]. While the detailed neural mechanisms behind these effects will require further investigation, this is the first case of recording chimpanzee brain activity in a very humane way (Figure 4).

Another recent study showed longitudinal brain development through structural MRI imaging, again using a relatively noninvasive technique. Chimpanzees can be anesthetized by injection in a face-to-face situation, as are human subjects.

Sakai and collaborators collected MRI images of the brain in three chimpanzees soon after birth [43] and continued for the first 6.5 years longitudinally. The chimpanzee data were compared with data from humans and macaque monkeys. The focus was a comparison of the developmental pattern of white matter (WM) within the prefrontal region, thought to mediate complex cognitive

![Figure 3](Current%20Opinion%20in%20Neurobiology.png)

Altruistic behavior in chimpanzees. A chimpanzee is giving a stick to another chimpanzee on demand. Photo provided by Shinya Yamamoto.

![Figure 4](Current%20Opinion%20in%20Neurobiology.png)

EEG recordings in a chimpanzee. The chimpanzee quietly sat on the chair and allowed the experimenter to put electrode patches on the skin of her forehead, top of the head. Photo provided by Satoshi Hirata.
Evolution of the brain and social behavior in chimpanzees Matsuzawa

Chimpanzees are good at capturing images rapidly as a whole, while humans are better at understanding the meaning of what they see. Chimpanzees apparently focus on any salient objects, neglecting the social context. In contrast, humans always recognize things within a social context, paying preferential attention to people, as agents. This is consistent with the fact that humans are highly altruistic and collaborative from a very young age.

Such differences in humans may be traced to the social organization of early hominids, especially the way they reared their offspring. Chimpanzees give birth to one infant at a time with an average inter-birth-interval of five years [48]. Chimpanzee mothers rear their young more or less alone. However, humans are cooperative breeders, raising the next generation through the collaboration of many adults.

The distinctive factor in human communication is, of course, language. However, it is important to appreciate the broader implications of the nature of language, such as its portability. Suppose that you have witnessed an event: language allows you to bring the experience back to your home-base. Because of language, you can share it with the other members of your family or community. Chimpanzee-like photographic memory may well aid individuals in their everyday life. Human adults appear to have lost this extraordinary ability for eidetic memory. However, language has helped us to collaborate with each other and, moreover, to share benefits communally. Thus, this may be one mechanism for how humans have evolved toward increased collaboration and mutual support. This kind of evolutionary pressure may have provided the basis for the development of the human brain with its unique functions.

References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- **of outstanding interest**


There have been a few studies investigating chimpanzee brain development even in the fetus [44,45]. The most recently published study used a noninvasive ultrasound technique [46*,47], and found that while the growth rate of brain volume accelerated throughout gestation in human fetuses, as expected, this was not so in chimpanzee fetuses through the later stages of pregnancy. This indicates that humans and chimpanzees differ with respect to the development of brain volume during the fetal period [46*]. Uniquely human encephalization already begins in utero (Figure 5).

Social brain hypothesis: trade-off between memory and language based on social life
Recent studies of cognition and behavior demonstrate clearly the difference between humans and chimpanzees.

processes through its reciprocal connections with posterior brain regions. Prefrontal WM volume in chimpanzees was immature and had not yet reached its adult level during pre-puberty, similar to what was observed in humans, but not in macaques. However, the rate of prefrontal WM volume increase during infancy was slower in chimpanzees than in humans. The results suggest a more developmentally protracted elaboration of neuronal connections in the prefrontal portion of the developing brain in chimpanzees, a pattern that likely existed in the last common ancestor of chimpanzees and humans. The rapid development of prefrontal WM in human infants may assist in the development of complex social interactions as well as in the acquisition of experience-dependent knowledge and skills, such as language acquisition and learning to use modern technology.

![Figure 5](http://www.sciencedirect.com)
6 Social & emotional neuroscience


This study revealed an interesting aspect of chimpanzee collaboration: helping behavior on demand. Chimpanzee A had a set of tools such as sticks, straw, rope, etc. Chimpanzee B, next-door was presented with a foraging task to solve, for example, a bottle of juice was placed out of reach so that chimpanzee B needed a stick to retrieve it. The results showed that chimpanzee A did not spontaneously help chimpanzee B. However, when chimpanzee B extended and waved a hand through a window between the adjacent rooms (in request) chimpanzee A gave the necessary tool to chimpanzee B.


Evolution of the brain and social behavior in chimpanzees Matsuzawa

41. Ludwig VU, Adachi I, Matsuzawa T: Visuoauditory mappings between high luminance and high pitch are shared by chimpanzees (Pan troglodytes) and humans. Proc Natl Acad Sci U S A 2011, 108:20661-20665.

This is the first study demonstrating the visuoauditory mapping of chimpanzees. Both humans and chimpanzees showed a strong bias toward choosing bright color when the high pitch tone was presented, and choosing dark color when low pitch tone was presented.


This study collected MRI imaging of brain development in three chimpanzees soon after birth. Brain development was recorded for the first 6.5 years longitudinally. The focus was a comparison of the developmental pattern of white matter (WM) within the prefrontal region. The prefrontal WM volume in chimpanzees was immature and had not reached the adult level during pre-puberty, similar to what was observed in humans, but not in macaques. However, the rate of prefrontal WM volume increase during infancy was slower in chimpanzees than in humans.


This paper revealed fetal brain development in chimpanzees using a noninvasive ultrasound technique. The growth rate of brain volume accelerated throughout gestation in human fetuses, but not in chimpanzee fetuses through the later stages of pregnancy. This indicates that humans and chimpanzees differ with respect to the development of brain volume during the fetal period.
