Symbolic representation of number in chimpanzees
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This paper aims to summarize the existing evidence for the symbolic representation of number in chimpanzees. Chimpanzees can represent, to some extent, both the cardinal and the ordinal aspect of number. Through the medium of Arabic numerals we compared working memory in humans and chimpanzees using the same apparatus and following the same procedure. Three young chimpanzees outperformed human adults in memorizing briefly presented numerals. However, we found that chimpanzees were less proficient at a variety of other cognitive tasks including imitation, cross-modal matching, symmetry of symbols and referents, and one-to-one correspondence. In sum, chimpanzees do not possess human-like capabilities for representation at an abstract level. The present paper will discuss the constraints of the number concept in chimpanzees, and illuminate some unique features of human cognition.

Introduction
Using the Arabic numerals 0 through 9, the chimpanzee Ai can represent both the cardinal and the ordinal aspect of number to some extent [1]. Similar skills have now been partially confirmed in six other chimpanzees [2,3]. A recent study has used numerical stimuli to demonstrate an extraordinary memory capability in young chimpanzees [3]. In contrast with the memory test, chimpanzees show poor performance in many other cognitive tasks that require some form of abstraction. The present paper will address the following five topics. First, it describes the logic and framework for the study of the number concept in nonhuman animals. Second, it reviews the long-running Ai project, focusing in particular on studies dealing with the symbolic representation of number. Third, it describes the extraordinary memory capacity that young chimpanzees possess for numerals. Fourth, it introduces common characteristics of the difficulties experienced by chimpanzees in various kinds of cognitive tasks. Finally, it discusses the number concept within the larger context of cognition, illuminating cognitive development in chimpanzees and the unique features of human cognition.

The Ai project: psychophysical measurement and the underlying logic
The Ai project – encompassing a series of studies whose principal subject has been a female chimpanzee named Ai – began when Ai, at the age of 1.5 years, first touched an experimental keyboard on April 15th 1978 [3–5]. The last in a succession of ape-language projects launched in the second half of the 20th century, the Ai-project was also the forerunner of a new research paradigm called Comparative Cognitive Science (CCS) [6]. CCS is the combined study of psychophysics and ape-language, using computer-controlled apparatus. In its original form, CCS aimed to compare perception, memory, and cognition in humans with those of closely related species such as chimpanzees. Crucially, such inter-species comparisons rely on identical methods: subjects, irrespective of species, use the same apparatus and follow the same procedure during testing.

Psychophysics is the classic psychological study of measuring human sensation, perception, memory, and cognition in general. Psychophysics tries to unravel the relationship between physical events and psychological events. Psychophysical researchers have established many laws, including, for example, Weber–Fechner’s law and Steven’s power law. There exist well-established methods for measuring the relationship between the stimuli presented and the corresponding internal psychological states. Thus, psychophysics can be extended to issues related to concept formation, such as the understanding of number.

The Ai project has two important features: the research presents humans and chimpanzees with exactly the same tasks so that their performance can be compared in detail, and that the research undertakes that comparison by using the methods of psychophysics. There is the synergistic connection between these two features for the enterprise of CCS. CCS aims to compare different species at the level of cognitive mechanisms, and it is the great virtue of psychophysical method that serves not only to describe the performance of humans and nonhuman animals but also to analyze that performance into its component mechanisms. By adopting psychophysical approach, you can go beyond questions of what trained
chimpanzees can do and ask how chimpanzees and humans do what they do: What cognitive capacities are shared by the two species and what capacities distinguish them.

Ai was the first chimpanzee who learned to discriminate the 26 letters of the alphabet during tests of shape perception and visual acuity [7]. She also mastered additional visual symbols such as specially devised geometric shapes (called lexigrams) and Japanese Kanji characters signifying different colors, in the course of experiments designed to examine her classification of various colors [8].

Ever since the beginning of the Ai-project, my colleagues and I have been focusing on the mathematical skills of chimpanzees rather than on any form of bilateral communication between humans and chimpanzees—the latter having been the central theme of previous ape-language studies. There were four reasons why we decided to concentrate on issues related to number concepts.

First, the world of logico-mathematical skills was small. Mathematical cognition is a part of human cognition in general, but the number system is narrower and more clearly and precisely defined in comparison to the linguistic system. The number system includes the levels of Integer that is a part of Real number, and that is a part of Complex number. The scales of the number system advance from Nominal to Ordinal, Interval, and Ratio scales. Therefore, focusing on the Integer, for example, we can examine both cardinal aspects ('one, two, three, four...') and ordinal aspects ('first, second, third, fourth...') of the number concept in chimpanzees. From the perspective of future work, we can examine the combination of numerical elements to create new meaning; such as putting 1 and 0 together to create ‘10’ in the decimal number system. Moreover, further questions open up regarding numerical operations such as addition and subtraction. These kinds of numerical manipulations can be viewed as corresponding to the syntactical structure of the language system.

Our second reason for focusing on number concepts was the accumulation of knowledge about mathematical thinking in human subjects. Several important papers had just been published about the child’s understanding of number, including Gelman and Gallistel’s landmark article [9]. These helped us to discern what we ought to study in chimpanzees. Since then, further studies on number concepts in humans have continued to shed light on many relevant issues and promoted our understanding of various aspects of numerical cognition (see reviews in [10–13]) including its neural mechanisms [14,15].

Third, a handful of studies had reported on topics related to the number concept in nonhuman animals, such as enumeration, quantity discrimination, and sequential responding. Today, much attention continues to be paid to the concept of number in nonhuman animals [16,17]. Various researchers have published studies that they described as tests of numerical competence in macaque monkeys [18–20], cotton-top tamarin [21], elephant [22*], parrot [23], pigeons [24], even salamanders [25] and bees [26*]. However, none of these compared the performance of human and nonhuman subjects directly, using the same methodology. Almost all the literature on nonhuman animals has focused on rudimentary forms of the number concept. By contrast, the Ai-project’s series of number concept studies stands out clearly for two reasons. First, it focuses on the symbolic representation of number using Arabic numerals. This symbolic representation allowed us to conduct direct comparisons between humans and chimpanzees. Second, we applied psychophysical measurements using a fully automated computer-controlled apparatus that completely excluded any kind of social cueing.

The fourth reason why we decided to concentrate on issues related to number concepts is the connection to the psychophysical approach. Most domains of human cognition are not yet amenable to psychophysical analysis, because the proper mathematical characterization of the cognitive domain is not clear. Number, however, is highly amenable to psychophysical analysis. Indeed, the Weber–Fechner’s law of psychophysics holds in the numerical domain.

**Cardinal and ordinal aspects of number and introducing zero**

Ai is the first chimpanzee who mastered the use of Arabic numerals to represent numbers [4]. She learned both cardinal and ordinal aspects of the number system. She used the numerals to label real-life items, shown to her in a display window, in terms of their numerosity. She also became proficient at responding to Arabic numerals in ascending order, selecting them from a touch-screen in the correct sequence. When the numeral ‘0’ was introduced, Ai mastered its use in both the cardinal and the ordinal domains; however, the acquisition process and the generalization tests in this case clearly highlighted the constraints of the symbolic representation of number acquired by the chimpanzee [1*]. Further detail on Ai’s experience with numerals follows below.

Cardinal number training began when Ai was about five years old. She had already learnt to use lexigrams corresponding to object and color names. Ai mastered the skill of naming 1 through 6, in addition to the naming of 14 objects and 11 colors. Although the ‘word order’ of describing a particular sample (such as ‘five red toothbrushes’) was free, she spontaneously adopted a favored sequence, assigning the object and color names first and then naming the number last. This rule of describing the
Patterns in the ease with which Ai acquired object, color, and numerical labels provide an interesting contrast. During the initial phase of learning to use visual symbols to label corresponding objects, Ai experienced considerable difficulties: the first two objects required a long period of training. However, once past this early hurdle, learning to name a third object became easier, and the fourth easier yet. The same pattern was evident in the case of color naming [8]. This suggests that the chimpanzee ‘learned to learn’ in terms of objects and color naming. On the contrary, no comparable improvement was observed in the case of numerical naming: the sessions required to reach the learning criterion did not decrease as the numerals 3, 4, 5, and 6 were successively introduced.

After becoming proficient at the numerical naming of real life objects, Ai learned to label white dots projected onto a touch-screen monitor [27,28]. Her range of numerosities and associated labels was also extended, up to nine. Transferring the task on to a fully automated, computerized system further allowed us to measure precisely Ai’s response latencies in numerical naming. We found that the response latency remained constant up to about five dots; thereafter we saw a gradual increase in the time taken to label progressively larger sets. At a look, this tendency reminded us of the two phases of numerical labeling in the case of human subjects, subitizing and counting. However, Ai’s response latency reached its maximum at eight dots, rather than the largest of the sets, at nine. In fact, this tendency was clear throughout the process of acquisition: The latency was always at maximum at \( n - 1 \) dots, when the largest set being tested was of size \( n \). This strongly suggests that instead of counting the dots one by one, the chimpanzee seemed to be performing analog magnitude estimation of the number of dots. Such magnitude estimation of quantity is well documented not only in chimpanzees [29] but also in other animals [18]. Of course, Ai’s performance does not necessarily imply that chimpanzees cannot count; it simply proves that it is not a straightforward task to teach them to solve problems by counting items one by one.

In addition to the cardinal aspect of number, we also trained Ai in the ordinal domain. First she learned to select Arabic numerals from 1 to 9 on a touch-screen, in ascending order [30]. After initial training with consecutive items, we introduced sequences of nonadjacent numerals—these tests revealed both a positional and a symbolic distance effect in Ai’s performance. The positional effect means that Ai’s latency to select the first item in a sequence was short when this item was a small number; she took longer to decide on the first item when this was large. The symbolic distance effect describes the finding that latency decreases when two numerals being compared are far apart (in terms of their position in the sequence); the task becomes more difficult when the numerals are close. In sum, Ai (as well as other chimpanzees we subsequently trained) clearly mastered the sequencing of numerals along the ordinal scale [30,31].

In a follow-up study, we attempted to add the number 0 to Ai’s repertoire, training her in the meaning of ‘zero’ first in the cardinal and then in the ordinal domain [1*]. She was initially required to use the numeral 0 to describe the absence of dots in the display frame. After she had learned to use zero in this cardinal setting, we introduced the numeral 0 in the ordinal sequence task. She did not spontaneously place the numeral 0 before 1; there was, thus, no immediate transfer of the meaning of zero from the cardinal to the ordinal domain. However, once again, these negative data do not imply that chimpanzees cannot possess the concept of zero—in fact, Ai eventually succeeded in mastering both the cardinal and the ordinal meaning of the numeral. Nevertheless, whether chimpanzees are capable of bilateral transfer between cardinal and ordinal domains of number remains an open question.

**Working memory of numerals in chimpanzees**

People’s general view of the chimpanzee mind is that it is inferior to that of humans [32]. My colleagues and I showed for the first time that young chimpanzees have an extraordinary working memory capacity for numerical recollection [33,2**]. Their performance was better than that of human adults tested on the same apparatus following the same procedure.

The subjects of this study were six chimpanzees, three mother–offspring pairs, including Ai. We started training the three young chimpanzees at the age of four years; the two mothers who were also naïve to the task received the same training in parallel. All of them succeeded in learning the sequence of Arabic numerals from 1 to 9, using a touch-screen monitor connected to a computer. A memory task called ‘masking task’ was then introduced, at around the time when the young chimps reached five years of age. In this task, after touching the first numeral, all other numerals were replaced by white squares. The subjects had to remember which numeral had appeared in which location, and then touch the squares in the correct ascending order. Ayumu, one of the three young chimpanzees, can memorize the nine numerals in 0.67 s. His performance is much faster and more accurate than human adults (Figure 1).

We next invented a novel variation of the memory test, the so-called ‘limited-hold memory task’ [2**]. In this task, after touching the initial white circle that served as
the start key to each trial, the numerals appeared only for a certain limited duration, and were then automatically replaced by white squares. We tested both chimpanzee subjects (Ai and her son Ayumu) and human subjects on three different hold duration conditions: 650, 430, and 210 ms.

The number of numerals was limited to five. In human subjects and Ai, the percentage of correct trials decreased as a function of hold duration. However, from the very first session, Ayumu’s performance remained at almost the same level irrespective of hold duration, and showed no decrement. Ayumu outperformed all of the human subjects in both speed and accuracy. Our most recent (unpublished) data show that Ayumu can remember eight numerals shown for only 210 ms with an accuracy of 80%. Such memory performance has never been obtained in human subjects, even after intensive training. Seeing is
belonging: Please enter the keywords ‘chimpanzee memory’ in YouTube.com’s search engine, and watch the 10-min video clip entitled ‘Ayumu’ that we have uploaded.

Not only Ayumu but also the other two young chimpanzees we tested showed the same extraordinary memory capability [2**]. Young chimpanzees thus appear to have an extraordinary working memory capacity for numerical recollection—better than that of human adults. The results may be reminiscent of the phenomenon known as ‘eidetic imagery’ or the feats of so-called ‘idiot savants’. Such abilities are known to be present in some human children among thousands, with the ability generally declining with age.

A recent study presented the first examination of eye tracking in chimpanzees by a computer-based automatic detection system [34*]. The eye movements of chimpanzees as they viewed naturalistic pictures were recorded. The results were compared with those of humans in the same apparatus following the same procedure. Although the two species shared many common features such as looking at faces and eyes, chimpanzees shifted the fixation location more quickly and more broadly than humans. The chimpanzees are good at quickly grasping the pattern as a whole.

Cognitive tasks that present particular difficulties for chimpanzees

During my past three decades with the chimpanzees [35], it became clear that some cognitive tasks easy for humans were not so easy for chimpanzees. For example, although infant chimpanzees show neonatal imitation of facial gestures just like humans, this does not develop into generalized imitation [36]. Chimpanzees can master the ‘Do this!’ game to some extent. Although they can imitate actions toward objects, it is difficult for them to imitate actions toward their own bodies, and even more difficult to imitate simple actions without objects [37].

Cross-modal matching is also a challenging task for chimpanzees. They require intensive training to master matching auditory stimuli to corresponding visual stimuli [38]. Similar difficulties can be observed in symbolic matching-to-sample tasks. Very little evidence exists regarding the symmetry of symbols and their referents. Let us consider a symbolic matching-to-sample task in which a referent needs to be matched to the corresponding symbol. For example, the color ‘red’ must be matched to the symbol ‘red’, and the color ‘green’ to the symbol ‘green’. After intensive training on the task, chimpanzees can become proficient at selecting the correct symbol in response to being presented with a specific color. In turn, you can now test the reverse scenario: showing a symbol first and then providing two choice alternatives, the color ‘red’ pitted against the color ‘green’. Chimpanzees, trained only on color-to-symbol matching, find it difficult to match the symbol to the corresponding color. This kind of bi-directional correspondence between symbols and referents is referred to as ‘symmetry’. Symmetry is almost automatically established in the early phase of human language development. However, this is not the case in chimpanzees, who do not transfer spontaneously but need further intensive training [39].

Let us return to the issue of number. In true counting behavior, one-to-one correspondence should provide the essential basis for further establishment of the number concept. Imagine that you place five cups upside down in front of a chimpanzee, and then provide her with small wooden blocks. Using a gesture, you then ask the chimpanzee to put the wooden blocks on top of the cups. It is extremely difficult for the chimpanzee to place the wooden blocks—which can be seen as representing ‘counters’—on the cups one by one. She will more probably stack the blocks on top of one another, the chimpanzees’ preferred way of manipulating objects in such situations. Of course, chimpanzees may learn to solve this particular task, however, it will not automatically generalize to variations thereof. One-to-one correspondence looks easy to us, but it is not so for the chimpanzees.

Human infants assume stable supine posture from right after birth [40*]. This enhances face-to-face visual communication, vocal exchange, as well as bimanual object manipulation since the hands are freed from having to cling to the mother. By contrast, chimpanzee infants continuously cling to their mothers at least throughout the first three months of life. It is the stable supine posture, not bipedal locomotion, that makes human hands free and provides important clues to the complexity of our object manipulation, a precursor of tool use. When we analyze the development of object manipulation in chimpanzees using standard tests involving wooden blocks, nesting cups, and so forth, we see interesting differences between the two species in terms of action grammar [41]. Only one of the three infant chimpanzees we studied started to stack blocks spontaneously—she did so at a little less than three years of age, much later than human infants [42]. The other two never stacked blocks, despite having had extensive experience of watching their mothers’ stacking behavior. No chimpanzees, not even Ai, succeeded in making a copy of a simple three-block structure, such as a ‘bridge’ or ‘arch’ in which two blocks are placed side by side a short distance apart and a third is placed on top of both [43*]. Chimpanzees can manipulate blocks into one-dimensional structures, in a vertical or horizontal alignment. However, they find two-dimensional structures difficult, and three-dimensional construction more difficult still. These kinds of hierarchical constraints are seen throughout all examples of object manipulation by chimpanzees both in the laboratory and in the wild [44–47].
Conclusions: a trade-off theory of memory and symbolic representation

Why do chimpanzees have a better memory than humans for immediately capturing visual stimuli? Why do chimpanzees have difficulties representing things at an abstract level? The existing data can be interpreted according to an evolutionary trade-off hypothesis [40]. The common ancestor of humans and chimpanzees five to six million years ago may have possessed an extraordinary memory capability. At a certain point in evolution, because of limitations on brain capacity, the human brain may have acquired new functions in parallel with losing others—such as acquiring language while losing visuospatial temporal storage ability.

Humans may have developed unique cognitive capabilities such as symbolic representation or the ability to handle abstract concepts. Imagine that you witness a creature that passes quickly in front of you. You notice that body is covered in brown hairs, and the creature has a white streak on its forehead and a black spot on its right front leg. This, in a sense, is one useful way of dealing with stimuli that you encounter. However, there might be a different way to view the world. On the basis of the various features you observed, you may summarize this detailed information and label the creature as a ‘horse’. This kind of representation may be efficient because it can save you having to memorize details, allow you to generalize the experience to similar encounters in future, and share the information with others. In the case of the number concept, there is adaptive value in being able to report the number of enemies, count the number of allies, and communicate about the number of potential prey.

Communication is likely to have been more important than immediate memory in the social life of early hominids. Humans are creatures who can learn from the experiences of others. The trade-off theory has support from not only a phylogenetic but also an ontogenetic perspective. In humans, youngsters often outperform adults on certain memory tasks. In the course of cognitive development, human children may acquire linguistic skills while losing a chimpanzee-like photographic memory [40]. This may be due to the time lag of myelination of neuronal axons in each part of the brain. It is known that the association cortex responsible for complex representation and linguistic skills develops more slowly than other primary areas. Further study on the mind–brain relationship will illuminate this kind of trade-off across phylogeny and ontogeny. In sum, the present paper summarized the potentials and constraints of symbolic representation of number in chimpanzees, as revealed through the medium of Arabic numerals and through comparative studies using humans undergoing identical test procedures. In conclusion, the number concept in terms of symbolic representation is uniquely human, and comparable levels of abstraction have yet to be demonstrated in the rest of the animal kingdom—even in our closest evolutionary neighbor, the chimpanzee.

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