

Working memory of numerals in chimpanzees

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Chimpanzee memory has been extensively studied [1,2]. The general assumption is that, as with many other cognitive functions, it is inferior to that of humans [3]; some data, however, suggest that, in some circumstances, chimpanzee memory may indeed be superior to human memory [4]. Here we report that young chimpanzees have an extraordinary working memory capability for numerical recollection — better even than that of human adults tested in the same apparatus following the same procedure.

Our subjects were six chimpanzees, three mother-offspring pairs. One of the mothers, Ai, was the first chimpanzee who learned to use Arabic numerals to label sets of real-life objects with the corresponding number [5]. The other five chimpanzees had also participated in many previous studies [6], but they were naïve to tasks employing numerals.

In 2004, when the three young reached the age of four years, we began to teach the mother-offspring pairs the sequence of Arabic numerals from 1 to 9, using a touch-screen monitor connected to a computer. In the numerical sequence task, each trial was unique, in which the nine numerals appeared in different on-screen positions. Accurate performance with 1–2–3–4–5–6–7–8–9 spontaneously transferred to non-adjacent sequences such as 2–3–5–8–9. All naïve chimpanzees successfully learned this numerical sequence task (See Video clip 1 in the Supplemental data available on-line with this issue).

A 'masking task' to test memory was introduced at around the time when the young became five years old. In this task, after touching the first

numeral, all other numerals were replaced by white squares. The subject had to remember which numeral appeared in which location, and then touch them based on the knowledge of numerical sequence. All five naïve chimpanzees mastered the masking task, just like Ai [7]. It must be noted that the chance level of this task is very low: $p = 1/24$ with four numerals, $1/120$ with five numerals, and so on, down to $1/362,880$ with nine numerals. In general, the performance of the three young chimpanzees was better than that of the three mothers (see Table S1 in the Supplemental data). Ayumu, Ai's son, was the best performer among the subjects (Figure 1

and Video clip 2). Humans were slower than all of the three young chimpanzees in the response (Figure S1 in the Supplemental data; Video clips 3 and 4).

We developed a new test called the 'limited-hold memory task' as a novel way of comparing the working memory of chimpanzee and human subjects. In this task, after the touch to the initial white circle, the numerals appeared only for a certain limited duration, and were then automatically replaced by white squares. Three different hold duration conditions were tested: 650, 430 and 210 milliseconds. The duration of 650 milliseconds was equivalent to the average initial latency of five-numeral masking

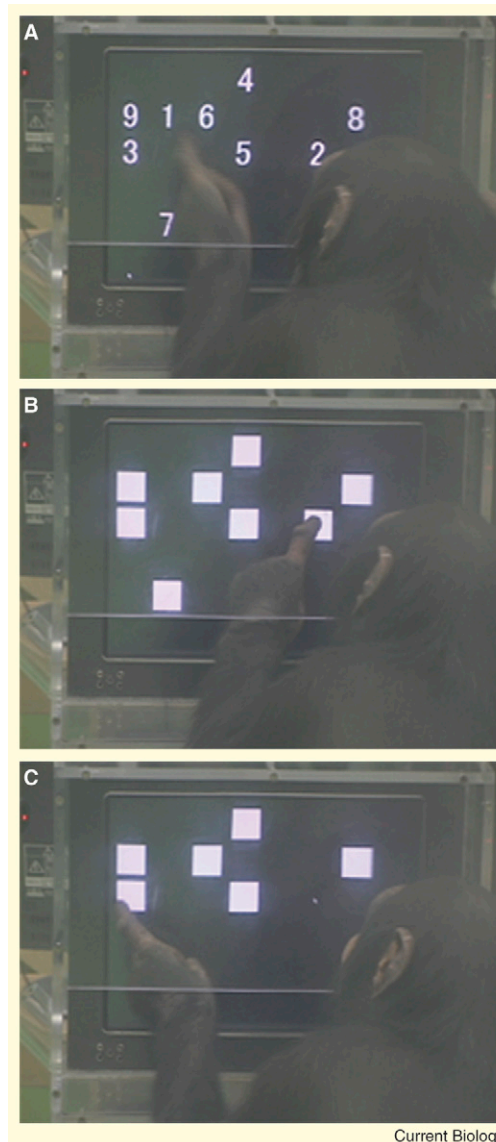


Figure 1. Chimpanzee Ayumu performing the masking task.

(A) Ayumu touches the first numeral of the sequence; (B) immediately thereafter the remaining numerals are replaced by white squares. (C) Ayumu remembered which number appeared in which locations on the screen.

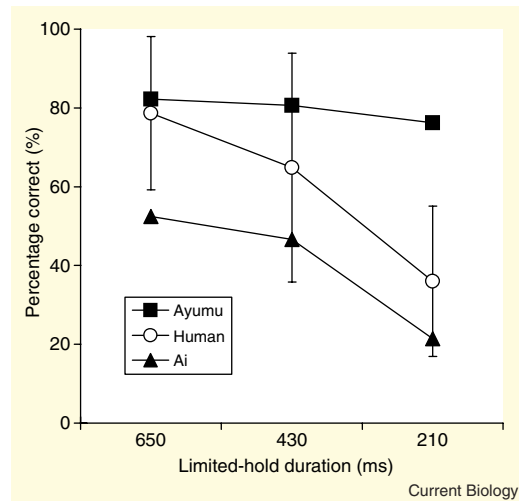


Figure 2. Results of the limited-hold memory task. The graph shows how Ai, Ayumu and human subjects ($n = 9$, the bars represent the SD) performed in the limited-hold memory task. The x-axis shows the three different limited-hold durations tested; percentage of trials correctly completed under each condition is shown on the y-axis. Each session consists of 50 trials. Each chimpanzee received 10 sessions and each of 9 humans received a single test session. A two-way ANOVA revealed that both main effects were significant (subjects: $F_{2,29} = 29.50$, $p < 0.001$, hold duration length:

$F_{2,29} = 121.45$, $p < 0.001$), as was the interaction between them ($F_{4,58} = 20.10$, $p < 0.001$). Post-hoc tests revealed that Ayumu's performance did not change as a function of hold duration ($F_{2,58} = 2.07$, $p = 0.136$), whereas Ai and the human subjects' performance decreased with shorter duration lengths ($F_{2,58} = 58.12$, $p < 0.001$, $F_{2,58} = 101.45$, $p < 0.001$, respectively). Pair-wise multiple comparisons by Ryan's method showed significant differences in performance between Ayumu and human subjects at the 430 milliseconds and 210 milliseconds hold durations ($p < 0.001$, respectively).

task. The shortest duration, 210 milliseconds, is close to the frequency of occurrence of human saccadic eye movement [8]. This means that this condition does not leave subjects enough time to explore the screen by eye movement. The limited-hold memory task provided a means of performing an objective comparison between the two species under exactly identical conditions. We compared Ai, the best mother performer, Ayumu, the best young performer, and human subjects ($n = 9$, all university students) in this task.

Figure 2 shows the results of the comparison between two chimpanzees and human subjects in the limited-hold memory task. The number of numerals was limited to five items. For example, the numerals 2, 3, 5, 8, 9 might appear very briefly on the screen and then be replaced by white squares. Subjects had to touch the squares in the correct order indicated by the original numerals.

In human subjects, the percentage of correct trials decreased as a function of the hold duration: the shorter the duration became, the worse the accuracy was (Video clip 5). Ai's performance was below that of

the human subjects' average, and showed the same tendency to worsen with shorter duration. From the very first session, however, Ayumu's performance remained at almost the same level, regardless of the hold duration, showing no decline comparable to that of the other subjects (Video clip 6, and Figure S2 in the Supplemental data). These data showed that the chimpanzee subjects can memorize at a glance the Arabic numerals scattered on the touch screen monitor and Ayumu outperformed all of the human subjects both in speed and accuracy.

Our results may be reminiscent of the phenomenon known as 'eidetic imagery' found by Jaensch [9,10]. Eidetic imagery has been defined as the memory capability to retain an accurate, detailed image of a complex scene or pattern. It is known to be present in a relatively high percentage of normal children, and then the ability declines with age. Our present study shows that young chimpanzees can quickly grasp many numerals at a glance, with no decline in performance as the hold duration is varied. Moreover, the young ones showed better

performance than adults in the memory task. Our study shows that young chimpanzees have an extraordinary working memory capability for numerical recollection better than that of human adults. The results fit well with what we know about the eidetic imagery in humans.

Supplemental data

Supplemental data, with video clips of the numerical and memory tasks of humans and chimpanzees, are available at <http://www.current-biology.com/cgi/content/full/17/23/R1004/DC1>

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References

1. Menzel, E.W. (1973). Chimpanzee spatial memory organization. *Science* 182, 943–945.
2. Fujita, K., and Matsuzawa, T. (1990). Delayed figure reconstruction by a chimpanzee (*Pan troglodytes*) and humans (*Homo sapiens*). *J. Comp. Psychol.* 104, 345–351.
3. Premack, D. (2007). Human and animal cognition: Continuity and discontinuity. *Proc. Natl. Acad. Sci. USA* 104, 13861–13867.
4. Tinklepaugh, O.L. (1932). The multiple delayed reaction with chimpanzees and monkeys. *J. Comp. Psychol.* 13, 207–243.
5. Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature* 315, 57–59.
6. Matsuzawa, T., Tomonaga, M., and Tanaka, M. (2006). *Cognitive Development in Chimpanzees* (Tokyo: Springer).
7. Kawai, N., and Matsuzawa, T. (2000). Numeric memory span in a chimpanzee. *Nature* 403, 39–40.
8. Bartz, A.E. (1962). Eye-movement latency, duration, and response time as a function of angular displacement. *J. Exp. Psychol.* 64, 318–324.
9. Jaensch, E.R., trans. by Oscar Oeser (1930). *Eidetic Imagery and Typological Methods of Investigation*, Second Edition (New York: Harcourt, Brace and Co).
10. Conway, A., Jarrold, C., Kane, M., Miyake, A., Towse, J., eds. (2007). *Variation in Working Memory* (New York: Oxford University Press).

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