relationships from memory represents a capacity that is homologous with humans (i.e. shared by common descent) or analogous (i.e. independently derived by convergent evolution), we need more information. For example, to determine whether Ai's capacity for numerical memory span falls within the range up to the magic number 7, she must be tested on numbers greater than 5, and must also be tested on non-numerical stimuli to assess whether the capacity is truly related to number or a more domain-general mechanism. Further, it would be interesting to look at Ai's scan patterns as she explores the initial display to see whether these differ as a function of the inter-integer differences. Another important issue is to determine whether her response is driven by visual memory or by setting up an initial sequence of motor responses, and then initiating them once the numbers are masked. This distinction between visual and motor memories is important, and critical to the homology/analogy problem. Another key area for further research will be to examine which areas of the brain are involved when she first calculates the correct numerical response and then, when she subsequently stores this information in memory for use in an explicit motor response. Are the brain areas recruited early in the learning of this task different from the areas used after extensive training, and how does this pattern of activity relate to that observed in young children? Finally, what are the limits on numerical memory span in animals, and to what extent does training influence such limitations? Uncovering the answers to these questions will bring us closer to understanding the depth of our shared cognitive heritage with animals.

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A conventional approach to chimpanzee cognition

Response to M.D. Hauser (2000)

Nobuyuki Kawai and Tetsuro Matsuzawa

Thanks to the failure of Clever Hans, the findings of numerical competence in non-human animals have been treated with caution by comparative psychologists. However, as summarized by Marc Hauser [Hauser, M.D. (2000) Homologies for numerical memory span? *Trends Cognit. Sci*. 4, 127–128][1], a growing body of evidence for non-human animals' numerical competence has been demonstrated, not only in primates but also in rodent and even avian species.

Besides numerical abilities, similarities in many other cognitive processes are found between humans and other animals. For instance, Wright and his colleagues have found evidence for both the primacy and the recency effects in the serial recognition task, in monkeys and pigeons as well as humans[2]. Despite several such parallels, however, comparative psychologists still seem wary of assuming the same underlying cognitive mechanisms in humans and animals. This is because a similarity in performance among different species can be superficial, and does not always indicate a shared cognitive process. It may be that the same task can be solved in qualitatively different ways by different species.

As Hauser points out, comparative psychologists need to distinguish 'homologous' processes from 'analogous' processes in cognition, particularly because humans might possess highly developed cognitive functions that are not shared with other species. How, then, can we distinguish homology from analogy?

As Hauser suggests, direct comparisons of the brain activation of human and other primate species may provide more information about the origins of human cognition. Recent advances in imaging techniques have suggested that chimpanzees might be suitable subjects for imaging studies. Rilling *et al*. took up this challenge to examine whether human and linguistically competent chimpanzees share homologous neural substrates during linguistic processing[3]. Two female linguistically trained chimpanzees were anesthetized and scanned (using ^{18}F-FDG PET) immediately after performing computerized speech and symbol comprehension tasks. Comparison of results with human subjects showed that different brain areas were activated in the chimpanzees and humans during these tasks, suggesting that there is little homology between the human and chimpanzee brain areas responsible for these aspects of linguistic processing (but see Ref. 4). Does this mean that analogous processes mediate human and chimpanzee 'language'? It is clear that we need more information, for despite within-subject reproducibility, even the two chimpanzees in this study exhibited different patterns of task-related brain activity. Such an inconsistent pattern of activation was attributed to their different rearing histories and it is known that the environment in which chimpanzees are raised has an important bearing on the development of later skills, such as symbol manipulation, tool use and so on.

Besides individual differences caused by rearing history, many practical problems prevent great apes from participating in imaging research. Because of their muscular strength and motion during scanning, apes need to be anesthetized, which does not allow a real-time recording of brain activity, and it also creates some risk for their health. Thus, there are many more hurdles to overcome before imaging studies using apes become a viable method of investigation.

How, then, can we track the origins of our cognitive evolution without investigating the ape brain? Until such time as reliable imaging techniques for great apes are developed, we can still effectively probe great ape cognition using conventional methods applied to human cognition; that is, analysis of response time and error patterns.

Tomonaga, Matsuzawa and Itakura analysed response times of their chimpanzee, Ai, in the numerical ordering task they developed[5–6]. They tested all 84 possible 3-digit combinations using the numerals 1 to 9 (i.e. 1-2-3,… 7-8-9), and found three major characteristics. First, as we also found in our study[7], Ai's response latency was longest when selecting the lowest number in a sequence, followed by much shorter response times for all the remaining numerals. The latter did not differ significantly from each other. These results suggested that Ai planned the complete sequence of presented numerals before making the first response. Second, her initial response time increased significantly as a function of the serial position of the first number to be pressed. In other words, higher numbers were selected with a greater latency than lower numbers when they were the first number selected. This was considered to reflect a serial-position effect. Furthermore, response time to the lowest number was faster when the inter-integer interval between the lowest and the second lowest number was larger. This effect was interpreted as the symbolic-distance effect.

Symbolic-distance effects are well documented in pigeons and monkeys as well as chimpanzees. However, findings of serial-position effects seem to be limited to primates. Terrace has suggested that monkeys build up an integrated linear representation by means of partial sequences, but that this is not the case in pigeons[8]. These phenomena are believed to reveal something about the nature of animals' cognitive representation of sequential learning.

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Although Ai seems to have an integrated linear representation of numerals, this does not necessarily mean that she has an ordinal scale for numbers. Further research that focuses on a transfer between ordinality and cardinality is needed. Aside from Ai's understanding of ordinality, Biro and Matsuzawa conducted an ingenious experiment to study her perceptual and cognitive mechanisms in solving a numerical ordering task[9]. In their experiment, a random set of three numbers from the range 0–9 (e.g. 2-5-7) was presented, spatially distributed on a touch-sensitive monitor. Ai was required to select the numbers in ascending order. On some trials, immediately after the correct selection of the lowest number in a series (2 in the above example), the positions on-screen of the remaining two numbers were switched by the computer. If Ai then selected the incorrect position of the second number, the screen automatically went blank. Her accuracy dropped to 45% correct on these 'switch' trials compared with 95% correct on the normal background trials.

Biro and Matsuzawa analysed her response times and found an interesting pattern. In the trials in which Ai scored correctly, the response latency from the first to the second number was longer than in the incorrect (switch) trials. In other words, response latency from the first to the second number was faster in the incorrect trials. Further video analysis revealed that Ai's error rate was higher when the first and second numbers were located in close proximity to each other. However, if there was some spatial separation between the first and the second number (which then switched to occupy the third number position), Ai could change her course to the other position. In almost half of all the incorrect trials, after the second selection, which resulted in the automatic clearing of the screen, Ai's finger continued to go to the third (now blank) position. The authors concluded that Ai had inspected all three numbers at the onset of each trial, decided the order in which they were to be selected, and planned the appropriate motor sequence that would lead to the correct response. This would account for the fact that the response time to the first (lowest) number was longer than to the remaining numbers.

We think this is similar to the human strategy during serial recognition tasks, and although we do not have information about how humans would solve this particular serial recognition task, we suspect their strategy would be similar to Ai's. It is, however, different from the way macaques solve the task. When Japanese macaques were taught to select different colored squares in a fixed order[10], they identified only the first target to be selected, and only after (and/or during) the selection of that target, which resulted in its disappearance, did they search for the next target to be selected. Therefore, the response times to subsequent targets decreased in a monotonic function.

We have now trained Ai to select different colored squares in a specific order, and can confirm that Ai builds an integrated linear representation for the order of colors (unpublished data), by showing transitive inference and symbolic-distance effects. We are now ready to test her memory span by presenting a set of colors instead of numerals. This will test her memory span for entities other than numbers, as Hauser suggests. We are also interested in whether her memory span falls within the seven items typically found in humans. One straightforward way is simply to increase systematically the number of items to be memorized, and we have started such an experiment. A related question is whether she can chunk groups of numbers with close proximity (e.g. 7-8-9 would gather as one 'chunk'), as humans do in numerical memory.

As Hauser points out in his commentary, we still don't know to what extent we share our cognitive abilities with chimpanzees or other primates. Some capacities will be homologous, but others might be analogous. Brain research may well provide answers; it has already provided much information about the nature of cognition. However, before the advent of brain research techniques, cognitive psychologists uncovered many aspects of human cognition by the analysis of reaction times and error patterns. We believe we can investigate to what extent chimpanzees share cognitive capacities with us by using homologous methods of studying cognition.

We wish to thank Marc Hauser for his comments, which have suggested some insightful new experiments. Inspired by his thoughtful comment, we have started some experiments with Ai that we hope will answer the questions he raises. We hope, too, that other researchers will provide further understanding of the evolution of human cognition and intelligence.

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