

just this issue by using false response labels in one of our experiments (Experiment 4). The results came as a bit of a surprise. One of us stubbornly reasoned that as a test for implicit learning of discriminative cues we should ask GY to respond using false response labels – that is, emotional labels that do not correspond to the emotions expressed in the stimuli. This might yield results showing that affective stimuli were labelled systematically and, thus, that associative learning had occurred. This was not found. Instead, when instructed with non-veridical alternatives, GY's performance was completely un-systematic and at chance level. Affective blindsight therefore does not appear to be explained by implicit learning. After all, it is unlikely that through untutored, unsupervised implicit learning GY would hit upon the correct solution – a solution that reflects a three-way equation between the stimulus, its conscious meaning and its non-conscious meaning.

The above considerations suggest that the issue of the relative sensitivity of various testing methods is more than a quantitative matter, and in fact involves a qualitative capacity for stimulus

identification. Heywood and Kentridge raise a very interesting issue when asking whether key-press responses could have strengthened the data further (in fact, that is what we did use). They speculate that with reflexive verbal responses, the response generated in the blind field via dedicated routes could be inhibited by mechanisms of awareness. The finding that non-veridical response alternatives have a negative effect on the results of guessing suggests, paradoxically, that awareness plays a role in covert recognition. For example, the underlying mechanism might be one of conscious processes monitoring autonomous reactions, as indeed Heywood and Kentridge suggest.

But there might be other reasons why indirect paradigms are more sensitive than direct paradigms and why different response modalities yield different results. Neuropsychological subjects are, by definition, unaware of the capacities that can be revealed by experiments on their implicit processes. 'Direct' methods require them to engage in discriminations that they do not believe they can make. In such a counterintuitive situation, subjects (and some experimenters!) might be less than willing to

accept that there is any point in continued vigilance with forced-choice guessing. Indirect methods completely remove this counterintuitive element.

Further research is needed to discover whether affective blindsight is restricted to emotions for which the amygdala is at present known to play a special role. But even if the amygdala's role is specific only to particular emotional stimuli or states, and other emotional states depend critically on other targets, our results suggest that these too can be assumed to be well-provided for in terms of visual projections via the sub-cortical collicular–pulvinar route (among others) that bypass the primary visual cortex.

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Homologies for numerical memory span?

Marc D. Hauser

For some, the case of Clever Hans represents the kind of trap that animal researchers often fall into when searching for human capacities in other creatures. Hans was certainly clever with respect to picking up on human cues, but was unquestionably clueless when it came to solving mathematical problems. Ever since the debunking of Clever Hans, however, an extraordinary amount of evidence has accumulated^{1,2}, showing beyond a shadow of doubt, that we share many of the core building blocks of our number capacity with other animals. We know, for example, that several avian (pigeon, African gray parrot) and mammalian (rat, rhesus monkey, chimpanzee) species can be trained to classify sets of objects with respect to their ordinal relationships, appreciate that number is property indifferent (i.e. as long as the object or event is an entity that can be counted or individuated, its properties are irrelevant), and that there is a one-to-one correspondence between the numerical tag and the object counted. There is also evidence that monkeys show a certain level of numerical sophistication in the absence of training. Specifically, using techniques that are analogous to those used with

human infants, cotton-top tamarins and rhesus monkeys have been shown to compute simple arithmetical operations such as additions and subtractions. Now, in an exciting new report in *Nature*³, Kawai and Matsuzawa add to our growing understanding of the evolutionary origins of the human capacity for number by showing that a chimpanzee has a numerical memory span that falls well within the range of the 'magic number 7', at least on some accounts⁴.

Kawai and Matsuzawa worked with their star chimpanzee, a female by the name of 'Ai' with over 20 years of experimental experience. Prior to conducting the current study, Matsuzawa had shown that Ai could learn the Arabic numerals from 0 to 9. Specifically, based on extensive training, Ai had learned to respond on a touch-sensitive monitor to the ordinal relationships between numbers. Thus, when shown a sequence of four numbers, with inter-integer differences of either one or more, she would touch each number from lowest to highest, and with remarkable speed and accuracy. Taking advantage of this ability, Kawai and Matsuzawa set up a memory span task. A set of numbers was displayed on a monitor, such as 1,3,4,6,9.

As soon as Ai pressed the first number in the sequence (i.e. 1), all of the remaining numbers were masked by a white square. Ai's task was to press the remaining numbers (now masked) in order. For set sizes of two to four numbers, her performance was above 90% correct. Although her performance dropped to 65% for set sizes of five, this was nonetheless significantly above chance (i.e. 4%; note that in the original manuscript this was incorrectly calculated as 6%). Of considerable interest was her reaction time to respond. Independent of set size, Ai was slowest on the first press, with reaction time remaining relatively constant for all subsequent responses. Thus, for example, mean reaction time for the first response to a set size of four was 717 ms, and then 390, 432, and 437 respectively for the last three, masked, responses. This strongly suggests that Ai first explored the number space, calculating the ordinal relationships and spatial locations of each number, and then used this stored information to guide her subsequent responses.

As in all well-designed research with interesting results, many questions remain. To understand better whether Ai's capacity for calculating ordinal

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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)

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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 humans². 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 processing³. Two female linguistically trained chimpanzees were anesthetized and scanned (using ¹⁸F-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 study⁷, 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 pigeons⁸. These phenomena are believed to reveal something about the nature of animals' cognitive representation of sequential learning.

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