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PROGRESS

Our chimpanzee mind

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Some might consider the title of this piece preposterous. Bishop Wilberforce would no doubt have shaken his fist at it, just as he disputed Huxley's championing of darwinian continuity. But the title of this essay is no more outrageous than one entitled 'The chimpanzee's bird brain', for there has been extensive evolutionary conservation of many neural and psychological functions across species. We share with chimpanzees some—but not all—mental functions, some of which are shared with other species as well. As the publication of the chimpanzee genome reveals, we also share a good deal of our DNA. Unfortunately, we are virtually in the dark when it comes to understanding how genes build minds. If comparative genomics is to enlighten our understanding of human origins, it must be accompanied by an equally rich description of animal psychology, both in terms of its underlying neural signatures and the evolutionary processes that led to convergence and divergence with other species.

Here I will focus on research in two domains of knowledge that have made considerable progress over the past five years: folk mathematics and folk psychology. What I mean by 'folk' is a sense of knowing that operates in the absence of education or other forms of culturally imposed experience—part of the brain's core knowledge[1,2]. Although the focus here is on comparisons between chimpanzees and humans, much of what follows is unlikely to be specific to chimpanzees. In fact, the bottom line at present is that for each psychological capacity explored, some other animal shares this ability with chimpanzees. The reason why chimpanzees may be uniquely placed to enlighten human origins is due both to their phylogenetic proximity to humans as well as the extent to which they have accumulated a suite of psychological abilities in the service of solving social and ecological problems that were largely shared with those faced by our hominid hunter–gatherers[3,4].

Folk mathematics

It might seem bizarre to ask about the evolution of mathematics, a system that originated with *Homo sapiens*. But this achievement did not emerge *ex nihilo*. Human adults and infants with no tutoring have at least two core, folk mathematical systems[1,5–7]. One operates by representing, in parallel, a small number (<5) of discrete objects or events. The second is unconstrained by magnitude, but its operation is approximate, constrained by the ratio between numbers. These two systems are not only present in chimpanzees, but evolved millions of years before the primates. What seems unique to humans is the integer list, a set of discrete symbols that enable us to quantify large numbers precisely.

A sense of number has a role in at least four naturally occurring contexts for chimpanzees and other animals: foraging, group hunting, food sharing and intercommunity warfare. Consider warfare. Along with humans, chimpanzees are among a handful of species willing to engage in lethal fighting (Fig. 1). Forty years of observations across Africa have shown that when three or more males from one community find a lone individual from a neighbouring community, they kill this individual. This ratio is meaningful, representing the minimum number of males necessary to hold and kill an intruder[9,10]. Experiments[11] confirm this numerical ratio and power asymmetry: if the loud call of a foreign male is played over a loudspeaker, groups of fewer than three males remain silent and still, whereas groups of three or more males call back and move towards the speaker in preparation for an attack.

Like other animals, the capacity for numerical quantification plays an essential role in the socioecology of chimpanzees. Whatever we discover in the laboratory, therefore, is unlikely to represent an artefact of testing, even though laboratory studies might reveal additional or more refined abilities owing to methodological differences.

An early demonstration of numerical ability in animals—and the large approximate system in particular—used an operant procedure with rats and pigeons[8,12]. After some number of events, such as light flashes or tones, animals depressed a key for food. The proportion of errors increased with the magnitude of the target number, with discrimination constrained by the ratio between numbers. A number discrimination problem with chimpanzees involved the sequential placement of individual food rewards into one of two concealed wells[13,14]. Success consisted of picking the larger of the two food quantities. Performance was significantly above chance with ratios of food quantity below 0.70, independent of absolute number. Like other species, chimpanzees show the signature of the large approximate number system.

Initial evidence of the small precise system in animals emerged from studies of rhesus monkeys. Using looking-time as a measure of expectation[15], animals looked for longer after a $1 + 1$ operation if the outcome was 1 or 3 than if it was 2 (refs 16, 17). Subjects failed to show a difference in looking time when the outcome was greater than 3 or when there were multiple addition operations; for example, rhesus monkeys looked for equally long periods of time at an outcome of 3, 4 or 5 following a $1 + 1 + 1$ operation[18]. These results reflect the small precise system, but not the large approximate system that is unconstrained by absolute number. Although studies of chimpanzees have yet to explore the small precise system, there is no reason to doubt its presence given evidence in other primates, including human infants.

Chimpanzee research departs from work on most other animals in training them to learn Arabic numerals[19–23]. I focus here on Matsuzawa's studies of the chimpanzee Ai because they are the most extensive, documenting both the acquisition of a number system as well as its limitations. After several years, Ai learned the first nine integers, acquiring an understanding of ordinality and cardinality. For example, when presented with three-to-five Arabic numerals on a monitor, Ai pressed each number in its appropriate ordinal sequence, independent of numerical distance. Like humans, however, Ai's response was fastest with greater distances, and the number of errors

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increased with smaller ratios—patterns that reveal the signature of the large approximate number system (Fig. 2).

Closer inspection of Ai's performance reveals a different number sense from our own. Ai's initial training required mapping '1' and '2' to the correct number of food rewards. When then tested on '3', Ai failed to generalize, applying it indiscriminately to arrays of two or three objects. The same thing happened with each successive number added to the list: extensive training, followed by a failure to generalize. Ai never learned the rule that each new Arabic numeral symbolized a new cardinal value. Human children do something different: their understanding of the first three integers emerges slowly, but once acquired (at about 3–3.5 years of age), children spontaneously generalize to the remaining set of numbers in the integer list[1,6]. Ai learned the integer list by associating each symbol with a discrete quantity. Human children, in contrast, first acquire an arbitrary list (the words for counting) and then make an induction from a limited sample to generate an infinite list of numbers.

We share with chimpanzees and other animals two core systems of folk mathematics. However, we depart from all other animals in our capacity to represent large numbers precisely. What enables this capacity, and much more, is presently unclear, but there are interesting possibilities on the horizon. For example, not all human cultures express the large precise system, even though their language is as expressive as any other natural language[24–26]. In these cultures, the two core systems are operative, with number words mapped on to the first few integers and then the use of 'many' for higher values. This raises the question of how particular aspects of our language faculty have uniquely transformed particular aspects of our thoughts. One possibility is that a set of computational mechanisms recruited by the language faculty (for example, recursive operations) is tapped by our mathematical faculty, allowing both systems the power of open-ended expression[27,28].

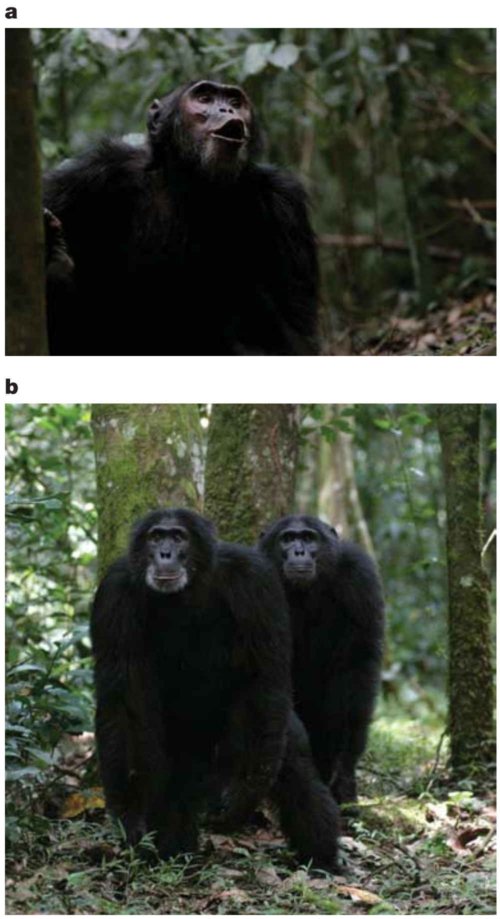

Figure 1 | Dangerous encounters. Chimpanzees compete with conspecifics both within and between communities. They may encounter members of other communities by hearing vocalizations of their neighbours (**a**), in which case they can become worried and their hair becomes erect (**b**). They can also see foreign chimpanzees during boundary patrols, when they make deep incursions into the territories of neighbouring communities. During such patrols, which are undertaken primarily by adult males, the chimpanzees are unusually silent and wary, and do not stop to feed. If they encounter chimpanzees from another community, fights may ensue and sometimes result in fatalities. Photographs courtesy of Kevin Langergraber at the University of Michigan, Ann Arbor, Michigan, USA.

Folk psychology

In parallel with the discussion of folk mathematics, we want to understand whether chimpanzees and other animals have a folk psychology, a system of knowing that enables individuals to infer what others believe, desire and want[29,30]. In our own species, these abilities gradually emerge over the first few years of life, reaching a celebratory crescendo at the age of 4–5 years. At this point, children can use the direction of eye gaze to infer what others know and to manipulate others' beliefs by lying.

The general consensus until the year 2000 was that animals, including chimpanzees, lacked all components of our folk psychology[31–33]. Povinelli's studies of chimpanzees provided the strongest support for this conclusion[34]. In these studies, a chimpanzee entered a test room and for each condition, begged for food from one of two experimenters. One experimenter could see the begging chimpanzee and the other could not, using body position, blindfolds, buckets and other devices to alter visual perspective. The chimpanzee begged equally from both experimenters, and never learned to beg selectively from only the experimenter who could see it. Povinelli concluded that chimpanzees fail to use seeing to infer what others know.

Using a different experimental approach, Hare and colleagues challenged Povinelli's conclusions[35,36]. Wild chimpanzees compete with each other more often than they cooperate. Povinelli's experiments involved cooperative communication between chimpanzee and human, but Hare's experiments involved competition between two chimpanzees of different dominance ranks, and were designed to test whether individuals use information about seeing to make inferences about knowing. Each condition imposed different

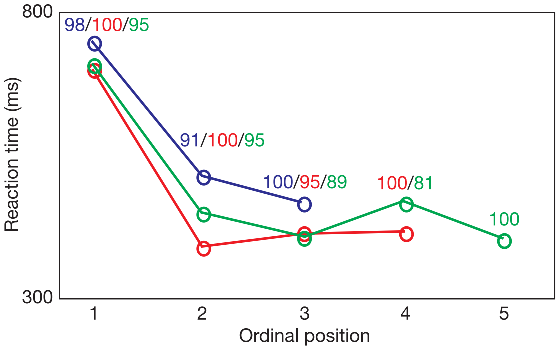

Figure 2 | The responses of chimpanzee Ai to a serial order task involving Arabic numerals. The *y* axis shows reaction times (in milliseconds) and the *x* axis shows the ordinal position of the number presented on the monitor. For example, '1' refers to the smallest number presented on the monitor, and the number that should have been pressed first in the ordinal sequence. If there were four numbers, '4' represents the largest number for the presented sequence. Blue symbols refer to three-item lists, red to four-item lists, and green to five-item lists. Above each cluster of points is the percentage of correct responses (that is, for contacting the correct number in the ordinal sequence, for three/four/five-item lists). Reaction time was slowest before the first selection, and then flattened out for the rest of the sequence, suggesting an initial planning stage. Graph generated from data presented in ref. 22.

constraints on what either one or both individuals could see. Consider three conditions in which the experimenter opened the door to the subordinate's room slightly before opening the dominant's door; this allowed the subordinate chimpanzee to make the first move in the absence of the dominant's behaviour (Fig. 3). Condition 1 involved one banana visible to both competitors, and one banana hidden behind an opaque barrier and visible only to the subordinate. Condition 2 involved placing one banana visible to both, and one behind a transparent barrier, so that both bananas were in view. Condition 3 involved two opaque barriers. While the subordinate chimpanzee watched, and the dominant chimpanzee looked away, the experimenter concealed one banana on the subordinate's side of the barrier. This condition differs from condition 1 in that it asks whether subordinates attend to the mere presence of a dominant or, more importantly, to what the dominant can see. If mere presence dictates competitive behaviour, then subordinates should stay put. In contrast, if subordinates recognize that the dominant chimpanzee failed to see the baiting of the food, then they should move out and pick up the concealed banana.

In condition 1, subordinates retrieved about half of the food, typically moving to the barrier before the dominant reacted. In condition 2, subordinates stayed put, allowing the dominant to run out and grab both bananas. The success of the subordinate chimpanzee in condition 1 was not attributable to physical protection from the barrier, as this would have worked equally well in condition 2. In condition 3, subordinates obtained more food than the dominants. Dominant chimpanzees could not see the hidden banana, which allowed subordinates to rush to the correct barrier. These and other results[36–38] show that chimpanzees can infer what another chimpanzee knows on the basis of what it sees.

Hare's results led to more penetrating studies of chimpanzees and other species, emphasizing the importance of using methods that tap spontaneous abilities and are sensitive to species-typical environments[37–41]. Results suggest that chimpanzees are equipped with some aspects of human folk psychology, but that they are not unique among animals. In fact, chimpanzees appear to be less adept than dogs at using the direction of eye gaze to infer the location of hidden food. Four questions direct current research. First, what is the nature of the chimpanzees' knowledge of the mental states of other chimpanzees? Second, to what extent is this knowledge a specialization for the domain of competition? Third, in what ways might chimpanzees differ from other animals? And finally, what specific abilities evolved in humans to enable our distinctive folk psychology, with its unlimited capacity to represent others' beliefs about beliefs?

Conclusions

We share with chimpanzees and other animals core aspects of folk mathematics and psychology. This conclusion sets up three broad questions that we can now begin to address. First, given the evidence for homology at the behavioural level, to what extent are there homologies at the genetic and neural levels? At the genetic level, the publication of the chimpanzee genome will lead to increased capacity to pinpoint homologies. However, we are woefully ignorant about how genes build brains, and how the electrical activity of the brain builds thoughts and emotions. The situation is nonetheless more promising today than it was five years ago, owing to the convergence of three disciplines: comparative genomics, animal psychology and developmental neuropsychology. For example, we are now beginning to understand the genetics of Williams syndrome and autism, deficits that strike at our folk psychology. By looking at the constellation of genes that underlie these disorders, their presence or absence in chimpanzees and other species, and the nature of each group's psychological limitations, the gap between genomics and psychology is shrinking.

Second, given the ways in which human and chimpanzee knowledge diverge, what computations uniquely enable human abilities? Many researchers implicate language, but the answer is unsatisfying without specifying the computational details. What we want to understand is how the language faculty or some other property of the mind, such as our capacity for storing and recollecting memories, enabled us to uniquely develop sophisticated mathematical tools, teach, and to pass down rich cultures through stories and written histories.

Third, although the behavioural repertoire of the chimpanzee is more like our own than any other species[3,4], the psychological mechanisms underlying chimpanzee behaviour seem to be largely

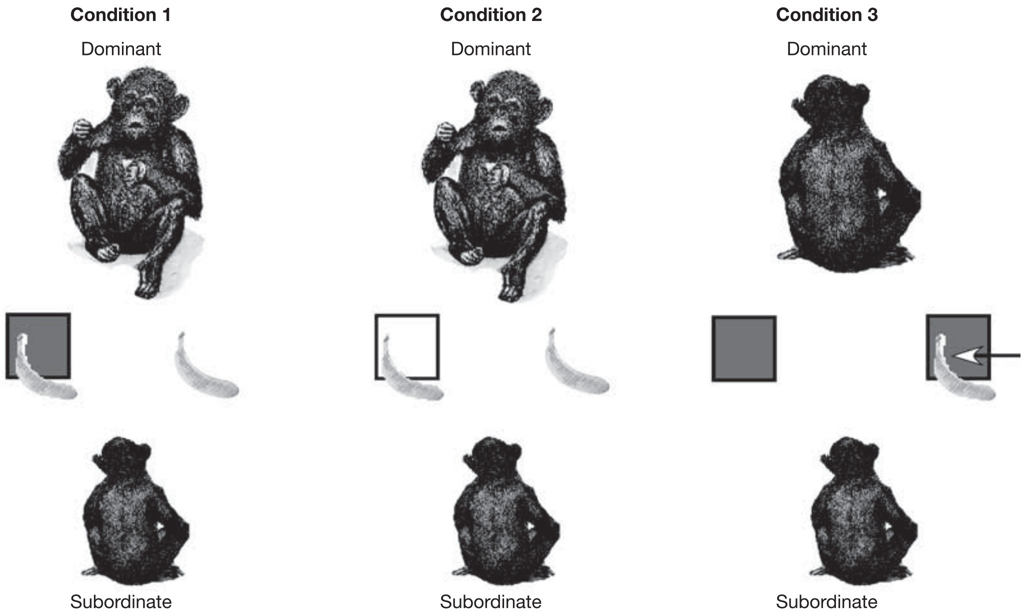

Figure 3 | Three conditions designed to test what chimpanzees know about seeing. In condition 1, one banana is visible to both the subordinate and dominant chimpanzee, but only the subordinate can see the banana behind the opaque screen. In condition 2, both the subordinate and dominant chimpanzee can see both bananas, as the screen is transparent. In condition 3, one banana is introduced behind the opaque screen while the dominant chimpanzee looks away. Adapted from refs 35, 36.

shared with other species. That is, for every cognitive mechanism explored in chimpanzees (beyond those of folk mathematics and psychology), there are parallels in other species. This means either that chimpanzees use a suite of shared psychological capacities to solve different problems from other animals, or that our analyses are relatively superficial. My bet is on the latter, given that the history of neuroscience reveals a high degree of coupling between particular socioecological pressures and adaptive solutions. With the welcome addition of comparative genomics to comparative neurobiology and behaviour, answers to these questions are indeed on the horizon.

1. Hauser, M. D. & Spelke, E. S. in *The Cognitive Neurosciences* (ed. Gazzaniga, M.) 1025–1147 (MIT Press, Cambridge, 2004).
2. Spelke, E. Core knowledge. *Am. Psychol.* **55,** 1233–1243 (2000).
3. Whiten, A. The second inheritance system of chimpanzees and humans. *Nature* doi:10.1038/nature04023 (this issue).
4. de Waal, F. B. M. A century of getting to know the chimpanzee. *Nature* doi:10.1038/nature03999 (this issue).
5. Butterworth, B. *What Counts: How Every Brain is Hardwired for Math* (Free Press, New York, 1999).
6. Carey, S. Evolutionary and ontogenetic foundations of arithmetic. *Mind Lang.* **16,** 37–55 (2001).
7. Dehaene, S. *The Number Sense* (Oxford Univ. Press, Oxford, 1997).
8. Gallistel, C. R. *The Organization of Learning* (MIT Press, Cambridge, 1990).
9. Manson, J. H. & Wrangham, R. W. Intergroup aggression in chimpanzees and humans. *Curr. Anthropol.* **32,** 369–390 (1991).
10. Wrangham, R. W. & Peterson, D. *Demonic Males* (Houghton Mifflin, New York, 1996).
11. Wilson, M. L., Hauser, M. D. & Wrangham, R. W. Does participation in cooperative intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Anim. Behav.* **61,** 1201–1213 (2001).
12. Platt, J. R. & Johnson, D. M. Localization of position within a homogeneous behaviour chain: effects of error contingencies. *Learn. Motiv.* **2,** 386–414 (1971).
13. Beran, M. J. Summation and numerousness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **115,** 181–191 (2001).
14. Beran, M. J. & Rumbaugh, D. M. “Constructive” enumeration by chimpanzees (*Pan troglodytes*) on a computerized task. *Anim. Cogn.* **4,** 81–89 (2001).
15. Wynn, K. Addition and subtraction by human infants. *Nature* **358,** 749–750 (1992).
16. Hauser, M. D., MacNeilage, P. & Ware, M. Numerical representations in primates. *Proc. Natl Acad. Sci. USA* **93,** 1514–1517 (1996).
17. Uller, C., Hauser, M. D. & Carey, S. Spontaneous representation of number in cotton-top tamarins (*Saguinus oedipus*). *J. Comp. Psychol.* **115,** 248–257 (2001).
18. Hauser, M. D. & Carey, S. Spontaneous number representations of small numbers of objects by rhesus macaques: examinations of content and format. *Cogn. Psychol.* **47,** 367–401 (2003).
19. Biro, D. & Matsuzawa, T. Numerical ordering in a chimpanzee (*Pan troglodytes*): planning, executing, and monitoring. *J. Comp. Psychol.* **113,** 178–195 (1999).
20. Boysen, S. T. & Bernston, G. G. Numerical competence in a chimpanzee. *J. Comp. Psychol.* **103,** 23–31 (1989).
21. Brannon, E. M. & Terrace, H. S. Ordering of the numerosities 1 to 9 by monkeys. *Science* **282,** 746–749 (1998).
22. Kawai, N. & Matsuzawa, T. Numerical memory span in a chimpanzee. *Nature* **403,** 39–40 (2000).
23. Tomonaga, M. & Matsuzawa, T. Sequential responding to arabic numerals with wild cards by the chimpanzee (*Pan troglodytes*). *Anim. Cogn.* **3,** 1–11 (2000).
24. Gelman, R. & Gallistel, C. R. Language and the origin of numerical concepts. *Science* **306,** 441–443 (2004).
25. Gordon, P. Numerical cognition without words: Evidence from Amazonia. *Science* **306,** 496–499 (2004).
26. Pica, P., Lemer, C., Izard, V. & Dehaene, S. Exact and approximate arithmetic in an Amazonian indigene group. *Science* **306,** 499–503 (2004).
27. Hauser, M. D., Chomsky, N. & Fitch, W. T. The faculty of language: What is it, who has it, and how did it evolve? *Science* **298,** 1569–1579 (2002).
28. Chomsky, N. *On Nature and Language* (Cambridge Univ. Press, New York, 2000).
29. Premack, D. & Premack, A. *Original Intelligence* (McGraw Hill, New York, 2002).
30. Premack, D. & Woodruff, G. Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* **4,** 515–526 (1978).
31. Cheney, D. L. & Seyfarth, R. M. *How Monkeys See the World: Inside the Mind of Another Species* (Chicago Univ. Press, Chicago, 1990).
32. Hauser, M. D. *Wild Minds: What Animals Really Think* (Henry Holt, New York, 2000).
33. Tomasello, M. & Call, J. *Primate Cognition* (Oxford Univ. Press, Oxford, 1997).
34. Povinelli, D. J. & Eddy, T. J. What young chimpanzees know about seeing. *Monogr. Soc. Res. Child Dev.* **247,** 1–147 (1996).
35. Hare, B., Call, J., Agnetta, B. & Tomasello, M. Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* **59,** 771–785 (2000).
36. Hare, B., Call, J. & Tomasello, M. Do chimpanzees know what conspecifics know? *Anim. Behav.* **61,** 139–151 (2001).
37. Call, J., Hare, B., Carpenter, M. & Tomasello, M. ‘Unwilling’ versus ‘unable’: chimpanzees’ understanding of human intentional action. *Dev. Sci.* **7,** 488–498 (2004).
38. Hare, B. & Tomasello, M. Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Anim. Behav.* **68,** 571–581 (2004).
39. Flombaum, J. & Santos, L. Rhesus monkeys attribute perceptions to others. *Curr. Biol.* **15,** 1–20 (2005).
40. Hare, B., Brown, M., Williamson, C. & Tomasello, M. The domestication of social cognition in dogs. *Science* **298,** 1636–1639 (2002).
41. Emery, N. J. & Clayton, N. S. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* **414,** 443–446 (2001).

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