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Working Memory: A Cognitive Limit to Non-Human Primate Recursive Thinking Prior to Hominid Evolution?

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Abstract

In this paper I explore the possibility that recursion is not part of the cognitive repertoire of non-human primates due to a limitation on the size of working memory in non-human primates such as the chimpanzees. Multiple lines of data imply that chimpanzee working memory may be of size 2. If so, they lack the cognitive capacity for recursive thinking. Implications that change in working memory size during hominid evolution may have had for changes in the basis for constructing social cohesion, and whether the cognitive difference between *Homo sapiens* and non-human primates is one of degree or kind, are discussed.

Keywords: working memory, recursion, primates, hominid evolution

Working Memory and Recursion

That there are significant differences in the cognitive capacities of *Homo sapiens* in comparison with modern day non-human primates species is self-evident. Less clear is whether the evolutionary development of the cognitive capacities of modern *Homo sapiens* derive directly from cognitive capacities already present, though to a lesser degree, in a common ancestor for *Pan* and for *Homo*, or instead significant cognitive capacities were introduced subsequent to the speciation event that genetically separated the pongids from the hominids. Claims that the difference is one of degree and not kind have been bolstered by data on both captive and wild primates that have laid to rest, one after the other, assertions such as tool-making, grammatically based means of communication and culture as qualitative differences that make *Homo sapiens* cognitively unique among the primates. Of these, culture has often been seen as providing the firmest evidence for a qualitative divide, yet even this has been challenged by behavior patterns among chimpanzees whose origin and spread is through non-genetic transmission based upon learning (whether by imitation, emulation or some other means) within a social context – characteristics that some claim are the key aspects of what constitutes cultural phenomena.

Though the evidence countering each of the claimed bases for a qualitative difference in cognitive abilities has enriched enormously our understanding of the cognitive capacities of our nearest non-human primate relatives, the debate has been flawed by focusing on the consequences of cognitive capacities and not on the underlying abilities. Data showing tool making and tool use by chimpanzees, for example, do not determine if their cognitive capacities for tool using and making suffice for the more complex tools produced by our

hominid ancestors. Evidence to the contrary can be seen in a sequence of increased complexity in tool making during hominid evolution that may reflect qualitative cognitive changes. According to Pigeot (Pigeot, 1991), early hominid stone tools (< 2.5 mya) such as Oldowan choppers are conceptually 1-dimensional as they are based on producing a cutting, or chopping, edge on a cobble. The conceptual framework for making stone tools then becomes 2-dimensional around 1.5 mya when the stone tools are conceptualized as having a two dimensional form mapped onto a stone object through flint knapping. Finally, with the introduction of the Upper Paleolithic blade tool industry, tool making conceptually incorporates a third dimension that enables control over the relationship between blade production and volume.

Similarly, when language performance is divided into the underlying cognitive and biological capacities invoked by *Homo sapiens*, the evidence for degree rather than kind is less clear-cut. In a review of language components divided into faculty of language (broad sense) and faculty of language (narrow sense), the components of the former are found to have homologues in animal communication but the latter, with recursion as its primary component, appears to be specific to *Homo sapiens* (Hauser, Chomsky, & Fitch, 2002). While a likely cognitive precursor to recursion, namely implicit rule learning, does occur with at least one non-human primate (cotton-top tamarins) when the rules represent a finite state grammar (Hauser, Weiss, & Marcus, 2002), the same is not true for phrase-structure grammars (Fitch & Hauser, 2004). Thus non-human primates appear to lack recursive reasoning and “little progress has been made in identifying the specific capabilities [underlying recursion] that are lacking in other animals” (Hauser, Chomsky, & Fitch, 2002).

In this paper I explore the possibility that recursion fails to be part of the cognitive repertoire of non-human primates due to a limitation on the size of working memory in non-human primates such as the chimpanzees. That the size of working memory of chimpanzees is less than the working memory of modern *Homo sapiens* is evident. Increase in the size of working memory may have had major consequences for hominid evolution (Russell, 1996) and it is possible that the cognitive consequences of a genetic change in the size of working memory is responsible for the profound changes that took place in hominid evolution during the Upper Paleolithic (Coolidge & Wynn, 2005).

To see the problem with recursion and a small working memory size, consider the way genealogical tracing is used recursively to compute the members of one’s family tree. Genealogical tracing begins by linking two persons – one’s

mother and one's father – to a target individual using a culturally defined notion of parentage. It is then applied recursively to each of these individuals. More formally, let us represent the mother linkage by a two-place predicate, $M(_, _)$, where for persons x and y the claim $M(x, y)$ is valid only if y is the person culturally identified as the mother of x . For a set S of persons, the predicate $M(x, _)$ applied to the set S , based on person x in S , consists of all persons y in S for whom $M(x, y)$ is true. So long as only a single person, y , is identified as the mother of x , we may write $y = M(x, _)$. We can now use the $M(_, _)$ predicate recursively to define a new two-place predicate, $MM(_, _)$ (mother's mother, or grandmother from the perspective of English speakers) by setting $MM(x, z)$ to be true if $z = M(M(x, _), _)$. This computation requires a minimum of three places in working memory: a slot for x , a slot for $M(x, _)$ and a slot for z , the outcome of doing the computation.

Chimpanzee Working Memory = 2

How small is the working memory of chimpanzees? Published data on chimpanzee (primarily *Pan troglodytes*) behavior both in the wild and in captivity suggest a limit of two concepts being held simultaneously in working memory during ongoing behavior, whether the chimpanzee is interacting with the physical or the social world. The lines of evidence are multiple: the cognitive challenges of nut cracking behavior, the length and frequency of gesture combinations, the length and frequency of token combinations in language learning experiments, the frequency and number of stone and nut objects acted upon under experimental conditions, the formation of dyadic but not triadic interactions, and the maximum number of number symbols memorized when testing for ability to recall number symbols. Each of these will be considered in turn.

Nut Cracking Behavior

Nut cracking by chimpanzees requires the manipulation of three objects: a stone anvil, the nut to be cracked and a stone used to crack the nut. The behavior is learned, not biological and some chimpanzee groups do not crack nuts despite their availability (McGrew, Ham, White, Tutin, & Fernandez, 1997). Of all the tool-based tasks engaged in by chimpanzees, nut cracking is cognitively the most demanding (Hayashi, Mizuno, & Matsuzawa, 2005; T. Matsuzawa, 1996) and cognitively beyond the capability of some individuals in a group of otherwise nut cracking chimpanzees. Data from wild-living chimpanzees in Bossou, Guinea and collected over a period of 16 years (see Table 1) show that no chimpanzee learns to crack nuts before 3 years of age and about 1/4 of the juvenile-to-adult chimpanzees

Table 1: Nut cracking at Bossou, Guinea (*Pan troglodytes*)

Crack Nuts ¹	Age < 3.0	Age ≥ 3.0
Yes	0	22
No	22	7

¹Data from (Biro et al., 2003)

have never cracked nuts: "If not learnt by the end of this period [3 – 5 years of age], the skill will not be acquired..." (Biro et al., 2003). The failure to learn to crack nuts is particularly significant since the non-nut cracking chimpanzees both observe the nut cracking chimpanzees and scrounge nuts from them, hence do not lack examples showing them how to crack nuts.

Chimpanzees who learn to crack nuts do so through observation of others (primarily one's biological mother) and through trial and error attempts at cracking nuts. Four stages in learning to crack nuts have been identified: (1) single-object manipulation at around one year of age, (2) object association manipulation involving two objects that begins around two years of age, (3) performing multiple actions, starting around three years of age such as placing a nut on an anvil and hitting it with a hand and (4) putting together the sequence of placing a nut on an anvil and hitting it with a stone hammer so as to crack it open (Tetsuro Matsuzawa, 1994). Chimpanzees who do not learn to crack nuts apparently are unable to put together the full sequence of actions needed to crack nuts despite repeated observations of nut cracking chimpanzees. The full sequence requires that three objects be manipulated simultaneously: (1) the anvil stone, (2) the nut and (3) the hammer stone. A working memory of size two with cognitively unequal implementation across individuals in terms of manipulating three objects would account for the failure of some chimpanzees to learn to crack nuts despite repeated observation of successful nut cracking chimpanzees.

The failure of 1/4 of the chimpanzees at Bossou to ever learn to crack nuts is matched by experimental evidence. Three naïve, adult chimpanzees who had previously not been exposed to nut cracking were exposed to human models of nut cracking at the Primate Research Institute of Kyoto University using nut cracking stones from Bossou (Hayashi, Mizuno, & Matsuzawa, 2005). Though the training session was relatively short, two of the three chimpanzees learned the necessary sequence for cracking nuts. The experimenters kept detailed records of all instances of the chimpanzees' interaction with either stones or nuts or both, thus providing data on the relative frequency of instances of nut cracking in comparison to the number of instances when the chimpanzees were involved with the stones and nuts (see Table 2).

Table 2: Experimental nut cracking, three naïve subjects

Number of Objects ¹	Ai	Chloe	Pan
1 stone or 1 nut	110	205	394
2 objects, stones and/or nuts	33	45	98
3 objects, stones and/or nuts	4	0	1
3 objects, nut cracking	0	21	23

¹Data from (Hayashi, Mizuno, & Matsuzawa, 2005)

Though the sample size $n = 3$ does not allow for meaningful statistical comparison, nonetheless it is intriguing that 1/3 of the experimental subjects did not learn to crack nuts in accordance with the proportion of non-nut cracking chimpanzees at Bossou. Interestingly, the chimpanzee named

Ai failed to learn to crack nuts despite the fact she previously “demonstrated remarkable abilities in a variety of cognitive tasks” (Hayashi, Mizuno, & Matsuzawa, 2005) (see below, Number Span).

Regardless of subject, the frequency of interaction events with stones and/or nuts drops off exponentially, suggesting a fixed transition probability between manipulating n and $n+1$ objects. If the nut cracking episodes are not considered, however, interaction with 3 objects seldom occurs. Thus nut cracking does not appear to arise out of behavior that would already involve three objects, but appears to make possible interaction with three objects through providing a focused, very specific pattern of interaction that also provides a reward in the form of the nutmeat from the cracked nut. These data, then, are consistent with the observations made at Bossou and provide evidence that chimpanzee interaction with objects, in the absence of a task such as nut cracking, may be limited to two objects at a time, suggesting a working memory of size two.

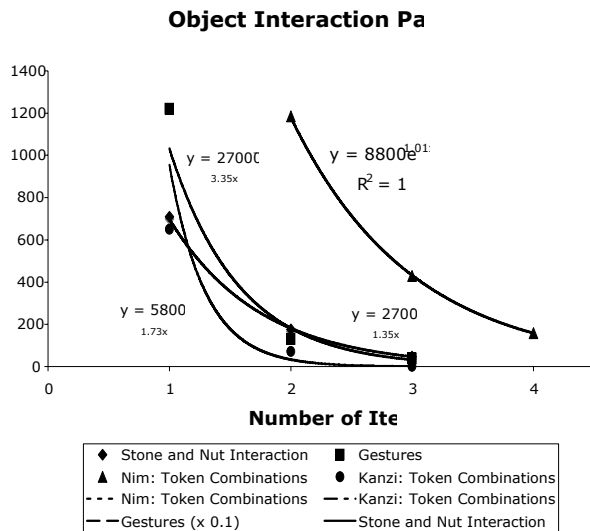


Figure 1: Exponential decrease in frequency of interaction.

Gestures

The pattern of rapidly decreasing frequency of interaction with the number of objects or events also occurs with data on communication events using gestures. Various gestures are used by chimpanzees in a social context for matters such as gaining attention or to solicit play by juveniles. The gestures used depend on the attention state of the intended recipient (Is the recipient facing the gesturing individual?) and gestures can be individually learned (Lilebal, Call, & Tomasello, 2004). Gestures are combined into sequences that “may represent strategies ... by combining gestures depending on the social goal the sender wants to obtain, and the recipient’s behavior” (p. 379).

Gestures for a group of 19 captive chimpanzees (*Pan troglodytes*) were recorded in detail and are summarized here with respect to the length of a gesture sequence (see Table 3). The frequency of length 3 gestures is greater than expected for an

Table 3: Gesture sequences

Length of Sequence ¹	1	2	3	> 3
Frequency	1,220	130	38	39

¹Data from (Lilebal, Call, & Tomasello, 2004)

exponential decrease in frequency (see Figure 1), but the longer gesture sequences are primarily due to repetition of the first gesture when it does not succeed in attracting the attention of the intended recipient. The authors comment: “chimpanzee gesture sequences may not be premeditated constructions, but rather are post hoc responses to an unresponsive recipient” (p. 394). These data are also consistent with the hypothesis that working memory is of size two.

Token Combinations

Two widely reported series of experiments on chimpanzees using symbol combinations with semantic content and based on self-generated syntactical rules provide data on the frequency with which combinations of tokens were formed under experimental conditions. One set of experiments used an individual from *Pan troglodytes* (Nim) and the other an individual from *Pan paniscus* (Kanzi). Whether the experiments demonstrate at least a rudimentary grammar in

Table 4: Token combinations, Nim and Kanzi

Number of tokens	Nim ¹	Kanzi Set 1 ²	Kanzi Set 2 ³	Analyzed Data (Set 2)
1 token	n.a.	39,793	13,691	(6,500)
2 tokens	11,845	n.a.	n.a.	723
≥ 2 tokens	--	2,540	1,422	--
3 tokens	4,292	n.a.	n.a.	> 8
≥ 3 tokens	--	n.a.	n.a.	n.a.
4 tokens	1,587	n.a.	n.a.	n.a.
> 4 tokens	1,487	n.a.	n.a.	n.a.

¹Data from (Terrace, Petitto, Sanders, & Bever, 1979)

²Data from (Savage-Rumbaugh, McDonald, Seveik, Hopkins, & Rubert, 1986)

³Data from (Greenfield & Savage-Rumbaugh, 1990)

the form of syntactical rules for symbol combination is not at issue here. Rather, the data will be summarized, as with the gesture data, in terms of the frequencies for the length of symbol combinations formed by Nim and Kanzi (see Table 4).

The frequency data for Nim decrease exponentially (see Figure 1). Combinations of three (or more) signs appear to be unstructured: “Nim’s three-sign combinations showed no evidence of lexical regularities, nor did they elaborate or qualify what he signed when he produced a two-sign combination” (Terrace, Petitto, Sanders, & Bever, 1979).

The Kanzi data have been interpreted as showing that Kanzi both uses syntactic rules and has semantic content for two-token combinations. The three-token combinations are

infrequent and (apparently) only 8 three-token combinations occurred more than once in the data set after questionable observations had been removed (see column 5, Table 4). The two-token combinations in column 5 represent 51% of the 1,422 combinations with ≥ 2 tokens (column 4, Table 4), so assuming the same rate of rejection for the one-token events, the analyzed data set had about 6,500 one-token events. This implies that the 8+ instances of three-tokens are well below the 80 three-token combinations that would be expected with an exponential decline in frequencies, even taking into the account uncertainty over the total number of three-token events produced by Kanzi (see Figure 1). Thus, even though the three-token events may have had syntactic structure and semantic content (Greenfield & Savage-Rumbaugh, 1990) and so the production of three-token events presumably had positive utility for Kanzi, Kanzi nonetheless was producing them at a much lower rate than would be expected in comparison with behavior by other chimpanzees. This suggests that the three-token events were not easy for Kanzi to produce. These data, then, are also consistent with the hypothesis that chimpanzee working memory is of size 2.

Interpersonal Interactions

Quantitative data on the frequency of dyadic versus triadic interactions among chimpanzees do not appear to have been published, but qualitative observations clearly indicate that triads are unusual. Chimpanzee communication has been characterized as unidirectional and only involving dyadic interactions (Tomasello, 1998); more specifically "chimpanzee gestures are used almost exclusively to regulate dyadic social interactions such as play, sex, and grooming, not to effect *triadic* interactions involving a partner and third entity, as is characteristic of human infants' early gestures and language" (p. 10, emphasis in the original). Similarly, Tomonaga et al. comment: "At present, we have not observed complex triadic exchanges among the mother-infant chimpanzees and objects which are based on "shared attention" or "reciprocity." It is still unclear as to whether this is a *cognitive constraint* or if this ability will emerge as the chimpanzees age" (Tomonaga et al., 2004).

Number Span

The last set of experiments to be considered here provides direct evidence on the size of working memory for *Pan troglodytes*. The chimpanzee Ai (see Table 2) was taught both to use Arabic number symbols (1 – 9) to represent the number of objects in a collection and to place any subset of them in order from smaller to larger. Her experimental task was to observe 5 Arabic numbers on a touch-sensitive computer screen and then to touch the location of the numbers sequentially from smaller to larger, but with the experimental condition that when the first number was touched all the other numbers disappeared from the screen. This meant that she had to touch the screen for the 2nd through the 5th number from memory. When presented with 5 numbers, Ai had about a 95% correct rate for recalling a string of 4 numbers correctly and about a 65% correct rate for a string of 5 numbers (Kawai & Matsuzawa, 2000b). When

the sequence was increased to 6 numbers she had about a 30% correct rate (Kawai & Matsuzawa, 2000a).

Though the authors interpreted these data as indicating that Ai has a working memory of 5, the data suggest otherwise. The last choice is forced; hence even if Ai were correct on 5 out of 5 numbers, only the 1st four numbers would need to be memorized. In addition, the first number is touched while all the numbers are visible on the screen and so it does not need to be memorized. Hence the sequence of 5 numbers only involves memorizing 3 numbers for correct performance. Ai's performance of 65% correct for the string of 5 numbers is only slight better than memorizing 2 numbers (numbers 2 and 3 in the sequence) and randomly guessing the 4th number, which would yield a 50% correct rate for the 4th number and so the string of 5 numbers would also be correct 50% of the time. The drop from 65% correct for the string of 5 numbers to 30% correct for a string of 6 numbers implies that the 5th number in the string of 6 numbers is a random guess. Thus these data imply that Ai has a working memory of 2. In addition, one commentator on these experiments independently concluded "chimpanzees might have a pure capacity of about 2.5 chunks on the average" (Cowan, 2000).

Working Memory Development

The chimpanzee data suggest that a maximum working memory size is reached around 3-4 years of age since chimpanzees do not learn to crack nuts after this age. We can compare this to data on the growth of working memory in *Homo sapiens*. Data from three separate studies (longitudinal (Diamond & Doar, 1989), age category (Siegel & Ryan, 1989) and both (Alp, 1994)) show a constant growth rate from 7 to around 144 months (see Figure 2). Assuming a chimpanzee working memory growth rate comparable to that of *Homo sapiens*, the growth trajectory predicts a working memory of 2 around 42 months for chimpanzees, namely the age when they are learning to crack nuts, and a working memory of 3 around 62 months for *Homo sapiens*, namely the age when children comprehend recursion based relative clauses (Hamburger & Crain, 1982) (see shaded areas in Figure 2).

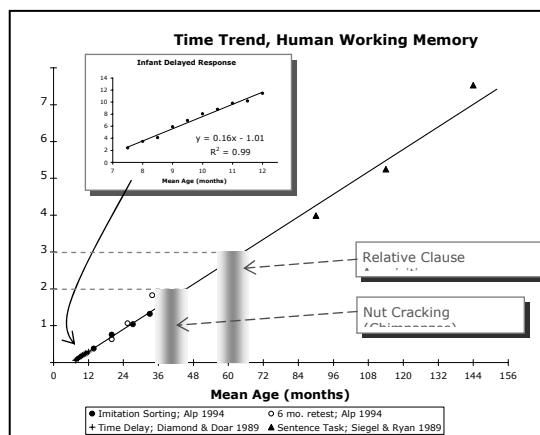


Figure 2: Trend line projected from Time Delay Response regressed on Infant Age (see inset). Constant term in a linear model for each study set to the same value to make each data set graphically comparable. Working memory scaled to WM = 7 at 144 months.

The developmental pattern is consistent with experimental work by Elman (Elman, 1993) on training neural nets to process complex sentences: "Training succeeds only when networks begin with limited working memory and gradually 'mature' to the adult state...successful learning may depend on starting small" (p. 71). Complementary work by Hurford (Hurford, 1999) on simulating the evolution of language acquisition proficiency adds an evolutionary perspective: "Whatever it is in the infant that 'starts small' and then grows, its growth facilitating language acquisition, the rate of this growth seems likely to be controlled in large part by genetic facts [and] ... is likely to be the product of Darwinian natural selection...the evolution of such a growing trait (here labeled 'working memory') can be modeled, with an adult value being reached around puberty" (p. 26). Hence the *Homo sapiens* developmental pattern shown in Figure 2 may be the evolutionary extension of a working memory developmental pattern for *Pan* that terminates around 42 months with a working memory of size 2.

Conclusion

The data reviewed here consistently point to a limitation in chimpanzee working memory below what is necessary for recursion to be possible. This would account for the lack of any obvious examples of recursive reasoning or activity on the part of non-human primates, including the experimental data on the tamarins showing that they do not infer phrase structure rules. Working memory, of course, is both more complex than what is implied by a single, numerical score and is not a unitary phenomenon but made up at least of visual, tactile and auditory components (Baddeley, 1986) common to both human and non-human primates with circuitry for these components located in the prefrontal and parietal cortex and in areas of sensory cortex (Pasternak & Greenlee, 2005). Human working memory, at least as modeled by Baddeley and elaborated on by Coolidge and Wynn (see Figure 1, 2005), also includes a phonological component and a central executive component, though a phonological component may not be part of working memory in non-human primates. Differences in working memory between non-human primates, such as the difference in working memory discussed here, and ourselves would have arisen through evolutionary processes acting on our hominid ancestors subsequent to divergence from a common ancestor with the African pongids.

The scope of some of these cognitive differences can be identified through changes in the cognitive abilities required for the production of the kind of stone tools made by our ancestors. For example, as noted earlier, Pigeot (1991) argues that stone tools are first conceptually one-dimensional for about a million years, then conceptually two-dimensional for an additional million or so years before the appearance of conceptually three dimensional blade tools during the Upper Paleolithic. Coolidge and Wynn (2005) have suggested that the florescence of material culture during the Upper Paleolithic may relate to a genetic mutation affecting the central executive component around 80,000 BP. Associated

with this florescence is the appearance of far more complex forms of social organization than occurs with the non-human primates.

More complex forms of social organization are linked to a change in the basis for maintaining social cohesion within and between social units such as residence groups. Social cohesion in non-human primate troops/residence groups is largely dependent on day-to-day and face-to-face interaction as a way to develop working relations among group members, whereas in human societies social cohesion arises through a system of culturally defined roles and role behavior. For small scale societies roles and role behavior are expressed through culturally constructed kin relations and expected patterns of behavior associated with these kin relations (Read, 2005). The system of kin relations is based on a recursive, generative logic (Bennardo & Read, 2005; Read, 1984, 2001, 2006; Read & Behrens, 1990) embedded within what anthropologists refer to as a kinship terminology. (A kinship terminology consists of the linguistic terms -- such as mother, father, brother, sister, husband, wife, ... employed by English speakers -- we use to refer to individuals culturally identified for us as relatives.)

The evolutionary impetus for this shift may stem from a socially destabilizing trend among non-human primates arising from increased individuation among the pongids in comparison to their cercopithecine ancestors. Increased individuation made social cohesion through face-to-face interaction problematic due to social complexity (measured as the number of unique individual and dyadic relations) expanding exponentially with growth in degree of individuation (Read, 2004, 2005). The solution to maintaining social cohesion while coping with increased individuation worked out by our hominid ancestors has its counterpart in hunter-gatherer groups. These groups maintain cohesion over hundreds of individuals and dozens of residence groups spread out over thousands of square kilometers through a culturally constructed system of kin relations and associated, expected patterns of behavior.

As shown by the data reviewed here, social cohesion based on kin relations using recursive logic could not have arisen without expansion in the working memory beyond that of our common ancestor with the African pongids. Without the cognitive ability to construct the kind of recursive, conceptual kinship system that underlies human societies, we must conclude that the cognitive difference between modern *Homo sapiens* and the non-human primates is one of kind and not just degree.

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