

UCLA

Other Recent Work

Title

Quantitative Differences Between the Working Memory of Chimpanzees and Humans Gives Rise to Qualitative Differences

Permalink

<https://escholarship.org/uc/item/6312d9mz>

Author

Read, Dwight W

Publication Date

2014-07-25

Quantitative Differences Between the Working Memory of Chimpanzees and Humans Give Rise to Qualitative Differences

Dwight W. Read
Department of Anthropology and
Department of Statistics
UCLA
Los Angeles, CA 90095

Abstract

A recent article argues that pure working memory in humans and chimpanzees have the same size. However, the data offered to support this claim show the opposite, namely that the size of pure working memory in chimpanzees is smaller than that of humans. In addition, extensive data show that the effective size of working memory in chimpanzees is much smaller than in humans. Altogether, there are quantitative differences in the size of working memory (pure or effective) between chimpanzees and humans leading to significant qualitative differences between them.

Introduction

In a recent article, Peter Carruthers (2013) argues that working memory in humans is homologous to that in non-human primates, with comparable parameters, so "that other primates (and perhaps all mammals) have pure retention abilities whose limits are similar to those of humans" (p. 10377). The difference between human and non-human primates with respect to working memory then lies, he suggests, in the ability of humans to resist interference when doing a task, the employment of an extensive imagination, the capacity to mentally rehearse action, and so on. While these are interesting aspects of the differences between human and non-human primate working memory, and while he has provided a useful summary of results that have been obtained regarding working memory in the non-human primates, lacking in his story is an adequate accounting of documented changes that took place in cognitive capacity during the evolution of the hominin ancestors of *Homo sapiens* that make us radically different from the non-human primates. Carruthers attributes the differences to content due to speech: "we can be confident that they [non-human animals] are systematically different from us in the *contents* that figure in their WM. The primary reason for this is that only humans are capable of speech" (p. 10377, emphasis added), but this is a rather impoverished notion of what distinguishes the cognitive repertoire of humans from that of non-human animals and implies, incorrectly, that until speech arose, the content of non-human animal WM and human WM would not be systematically different. However, as Overmann *et al.* (2012) observe: "About 1.8 million years ago [before

speech] ... *Homo erectus* strikes a rock against another while holding the idea of a shape in his mind. Through a series of skillful choices of angles and strikes, he imposes that shape to produce a handaxe ...” and then they comment: “it is unlikely -- impossible, really -- that another species could conceive and execute the complex planning inherent in [this scenario] There is something else at play: an ability to construct and carry out increasingly elaborate plans of action” (p. 38). The difference between the handaxes made by our *Homo erectus* ancestors and the tools, such as termite sticks, made by chimpanzees is not simply due to humans having greater dexterity and ability to utilize more advanced hand-eye coordination than chimpanzees, but relates more fundamentally to having the cognitive capacity to implement the increased conceptual complexity required by the former for its production (Wynn 2002; Read and van der Leeuw 2008). Topologically, a handaxe requires that the toolmaker be able to conceptualize how a closed line (the edge of the handaxe) would divide a cobble or nodule into two parts (the top and bottom sides of the handaxe) and to modify these two parts conceptualized as closed, bounded, intersecting surfaces (Wynn 2002). This requires that the handaxe be visualized in two dimensions considered simultaneously. In contrast, termite sticks and other tools made by chimpanzees are derived from forms already present in the raw material and then brought to the foreground by, for example, the removal of leaves or side branches from the main branch when making a termite stick. For tools like this, the ultimate form is already present in, for example, the branch broken off from a tree or bush; for the handaxe, though, the ultimate form does not exist except conceptually and must be imposed. A handaxe thus requires a far more complex conceptualization for its realization and this depends upon expansion in at least the effective working memory size, if not the absolute working memory size, for its realization (Read and van der Leeuw 2008). Missing in Carruthers’ story, then, is a credible accounting of this remarkable difference in the cognitive ability of humans and their hominin ancestors in comparison to the non-human primates and how this relates to differences in working memory capacities and not just to content — a difference that underlies the qualitative differences in cognitive abilities evident between our hominin ancestors and the non-human primates; differences that can already be seen in the earliest evidence (around 2.5 - 3.0 mya) we have for artifacts produced by hominins (Read and van der Leeuw 2008 and references therein).

Homology Between Human and Non-Human Working Memory

Carruthers' main conclusion is that working memory in non-human primates (henceforth WM* for non-human primates) is not only homologous to working memory in humans (henceforth WM) but WM* and WM have the same size; however, the claim that (size of WM*) = (size of WM) is not justified by the evidence presented in support of this claim and is contradicted by other, published evidence. The claim also leads to the paradox noted by Carruthers that while the size of WM* is supposedly the same as the size of WM, non-human primates perform qualitatively less well than do humans.

That working memory in humans evolved out of the working memory for a common ancestor of an extant great ape species and of humans — generally assumed to be the common ancestor to *Pan troglodytes* and *Homo sapiens* (Chapais 2008) —, is evident, hence chimpanzees and hu-

mans have homologous and not analogous working memory systems. Thus the point at issue is not whether WM is evolutionarily homologous to WM*, but whether the non-human primates and humans each have the same value for the size of their respective working memories.

Carruthers frames his affirmative answer to this question by using an ordinally organized list of possible comparisons between non-human primates and humans that goes from Level 1: WM in humans does not have a counterpart in non-human primates, to Level 9: WM* = WM. Carruthers includes the size of WM and the size of WM* as the second level in his ordinal scale, which misleadingly suggests that difference in size of working memory plays a limited role in the difference in performance between humans and, for example, chimpanzees. It is possible that the differences between humans and chimpanzees are due primarily to $(\text{size of WM}^*) < (\text{size of WM})$, with WM and WM* homologous and otherwise sharing several of the attributes in the ordinal sequence. Hence we need to review the evidence regarding the size of WM* and WM.

Measurement of the Size of Working Memory

There are two ways in which the size of working memory has been measured (Cowan 2010). One, used by Miller (1956), focuses on the *processing-related* size of working memory and leads to the widely quoted working memory size for humans of 7 ± 2 . The second focuses on the *storage-specific* capacity of working memory, which leads to a capacity for humans of 4 ± 1 (Cowan 2001). A useful way to consider the processing-related size of working memory is as a measure of the effective, as opposed to absolute, size of working memory, which would be the storage-specific capacity of working memory. I will refer to the numerical values obtained from the first measure as the *effective working memory size* (EWMS). I will follow Carruthers and refer to the numerical values obtained from the second measure as the *pure working memory size* (PWMS).

This distinction (also made by Carruthers) is important since PWMS is, roughly, equivalent to the number of registers in the CPU of a computer and does not take into account the logical circuitry through which PWMS is implemented. The latter leads to the effective performance measured by EWMS. The same PWMS may give rise to different effective working memory sizes, as Carruthers discusses. For my purposes here, though, I am concerned primarily with the effective working memory size since one of the critical concerns when comparing human to non-human primates is the difference in their performance. Also, from a pragmatic viewpoint, there are, to date, no good measures of PWMS*.

For the same reason that we distinguish PWMS from PWMS*, we also need to distinguish between non-human primates and humans when referring to EWMS. Notationally, I will use EWMS* when referring to non-human primates and EWMS when referring to humans. The essence of Carruthers' argument, then, is that $\text{PWMS}^* = \text{PWMS}$ but $\text{EWMS}^* < \text{EWMS}$ when comparing non-human primates and humans, with differences in these measures largely stemming from differences in verbal ability: "What is unique to humans [with regard to WM] is our

ability to vastly extend the topics and forms of reflective thinking in which we can engage by virtue of our capacity for mental rehearsal of speech” (Carruthers 2013).

Size of Human Pure Working Memory > Size of Chimpanzee Pure Working Memory

Now consider the evidence marshaled to show that $PWMS^* = PWMS$. As we will now see, the two data sets referenced by Carruthers for showing that $PWMS^* = PWMS$ do not validate that claim.

(1) The first data set involves "a test [Botvinik et al. 2009] of serial recall of position conducted with a macaque monkey, modeled on tests that have been used with humans" (p. 10373) that allegedly shows similarity in parameter values, though Carruthers admits that the data "would be consistent with a claimed WM limit of one to two items [i.e., $PWMS^* = 1$ or 2]" (p. 10373). Further, he does not mention that the macaque's performance degrades markedly after recalling the first position. Thus for the third position to be recalled in the experiment, the macaque was only correct 50% of the time (sequence of 4 items to be recalled) or 60% of the time (sequences of 3 items to be recalled), whereas humans would be correct about 100% of the time when recalling the 2nd and 3rd serial positions. While these data support the idea that working memory in macaques is homologous to working memory in humans, they do not support, as he admits, the claim that $PWMS^* = PWMS$.

(2) The second data set involves an experiment (Hauser *et al.* 2000) that supposedly is "not so easily critiqued" (p. 10373). In this experiment, Rhesus monkeys were able to consistently distinguish between a collection of 2 versus 3 food items, a collection of 3 versus 4 food items, but not between a collection of 3 versus 5 food items. Carruthers goes on to comment: "One might wonder why these data do not demonstrate that monkeys have a WM limit of seven (three items in one container and four in another) rather than four. The answer is that comparisons between containers benefit from chunking and do not just reflect raw retention limits" (p. 10373). However, chunking by non-human animals only occurs after hundreds of training trials (Moher *et al.* 2012 and references therein), whereas the Rhesus monkey experiment excluded training sessions and 75% of the trials were done but once by the test animal. The remaining trials were done just once before, a year earlier, for the remaining test animals. Chunking, then, does not appear to be a viable explanation for their performance. Also, chunking by human infants requires that they be given multiple, redundant chunking cues (Moher *et al.* 2012), whereas the Rhesus monkey experimenters added a slice of apple to an opaque jar sequentially, hence no visual cues for chunking were available. In addition, even if chunking were taking place, it is not evident how the Rhesus monkeys could then mentally compare the magnitudes of the chunked set of apple slices in one jar to the magnitude of the chunked set of apple slices in the other jar without some (unspecified) means to disambiguate the chunks back into their individual constituents to make the comparison (Feigenson and Halberda 2003). Finally, similar experiments with great apes show they they, unlike the Rhesus monkeys, can discriminate sequential comparisons beyond size 4 (Hanus and Call 2007). The experimenters comment: "in contrast to the rhesus macaques in Hauser et al.'s (2000) study, here we could not appreciate any clear performance breakdown

for quantity discriminations that went beyond three or four items [and] ... the current data can be explained without hypothesizing different mechanisms for processing small and large quantities as claimed by the subitizing or the object file model” (2007). The great ape data show, then, that whatever is being measured by the maximum length of the sequences for the food items that can be discriminated, whether by Rhesus monkeys or great apes, it is not PWMS* since the great apes discriminate sequences longer than 4 items, but their PWMS* is at most 4.

Hanus and Call (2007) attribute the performance of the great apes to an analogical system for estimating quantities, rather than a subitizing (or a discrete object file) model that seems to characterize the performance of the Rhesus monkeys. Subitizing (see Piazza 2010 for a recent review) refers to the wide-spread phenomenon in human and non-human animals whereby comparing the sizes of collections up to 3 or 4 items, but not larger, is done neither by counting, nor by a conscious 1-1 matching of the two collections, nor by a size estimation procedure, but by a more Gestalt, non-conscious comparison procedure (von Glasersfeld 1982). How subitizing takes place, though, is still uncertain (Pagano *et al.* 2014).

Attributing subitizing as the basis for the performance of the Rhesus monkeys leads, however, to the objection that subitizing experiments require the subject to compare the size of two collections of objects, with all objects in a collection shown simultaneously, whereas the Rhesus monkeys only see the slices of apple being introduced into an opaque jar sequentially. However, if subitizing is based on a “hard-wired,” innate 1-1 matching system, it may not be critical whether the items in a collection are shown simultaneously or sequentially. (For humans other than infants, a sequential presentation obviously allows for counting as the basis of comparison, hence the need for simultaneous presentations kept short enough to make counting impossible.) The fact that the performance of the Rhesus monkeys precisely parallels the performance that occurs with subitizing suggests that something like subitizing, allowing for a sequence to be represented through some kind of representation of numerosity, rather than remembering the specific items in the sequence, which is bounded in its extent by PWMS*, may be the critical factor for the performance of the Rhesus monkeys.

Even if the performance of the Rhesus monkeys is due to something like subitizing, it might still be countered that subitizing could just be an indirect measure of PWMS*. Were it the case that subitizing performance correlated strongly with PWMS, then whether the Rhesus monkeys were comparing the number of food items through something like subitizing or by some other means would not be critical for measuring PWMS*. Though it has been suggested (see Cutini and Bonato 2012) that subitizing in humans may relate to visual short term memory since human visual short term memory is of size 4 and humans easily subitize collections up to size 4, this does not account for the performance by the Rhesus monkeys, as their visual short term memory is about one-half the size of the visual short term memory for humans (Elmore *et al.* 2011: Fig 2A), hence they should only be able to deal with collections of size 1 or 2 if the size of visual short term memory is the basis for their performance.

Taking all of this together, we may conclude that the experiment by Hauser *et al.* does not provide us with a measure of PWMS* for Rhesus monkeys.

Developmental Trajectory for PWMS and size of PWMS*

Another difficulty with the claim that $PWMS = PWMS^*$ for the chimpanzees is that difference in the time spans for the growth in the size of PWMS in humans versus chimpanzees would yield different final values for PWMS. To see this, consider first the time span for growth of PWMS in humans.

The onset of active working memory in human infants starts as early as 5.5 months (Reznick *et al.* 2004) with $PWMS = 2$ for infants of age 5 - 7 months (Feigenson 2007 and references therein; Mohler *et al.* 2012 and references therein), though others (e.g., Kaldy and Leslie 2003) argue that $PWMS = 1$ for this age range. By age 10 - 14 months, PWMS has increased to 3 (Feigenson and Carey 2005 and references therein; Moher *et al.* 2012 and references therein) and PWMS then increases further to its mature working memory size with $PWMS = 4$.

While growth in EWMS does not match the pattern for increase in brain size during human development (Read 2008), the increase in PWMS should, however, relate to growth in brain size since PWMS refers to the architecture of the brain rather than to the implementation of that architecture: “The prefrontal cortex of the brain and the executive functions it supports undergo a long period of development in human ontogenesis, the fastest development occurring in the child’s first years of life.... Out [*sic*] data support the existence of continuity in the development of the mechanisms of working memory associated with activity in the prefrontal cortex of the brain during the first years of the child’s life.” (Tsetlin *et al.* 2012:698). Since rapid brain growth ceases after age 36 months (see Figures 1 and 2), we may (conservatively) assume that the adult value of $PWMS = 4$ is reached by age 36 months, at most.

Over the time period from 6 months to 36 months, there is virtually a perfect correlation between the growth trajectory for PWMS and increase in brain size measured by brain weight for males, with a slightly less strong correlation for females (see Figures 1 and 2). If we extrapolate backwards from 6 months to birth, we get a predicted value of $PWMS = 1$ at birth for humans with a brain weight about 400 grams. The growth trajectory in PWMS implies, then, an increase of 1 unit in PWMS for each 400 grams of brain weight. That brain weight does not reach 800 grams until age 12 months may account for why some researchers find that $PWMS = 1$ at age 6 months, while others find that $PWMS = 2$ at that age (see references above), since the brain weight would be about 600 grams at 6 months, hence in a cohort of 6 month old infants, PWMS would still be in transition from $PWMS = 1$ to $PWMS = 2$ and so the difference between research groups may be due, in part, to a sampling effect.

Next, we can apply these results to the time span and amount of growth in brain weight in chimpanzees. Chimpanzees have an average brain weight at birth of 151 grams and an average adult brain size of 382 grams (DeSilva and Lesnik 2006). Using human data of 1 unit of PWMS per

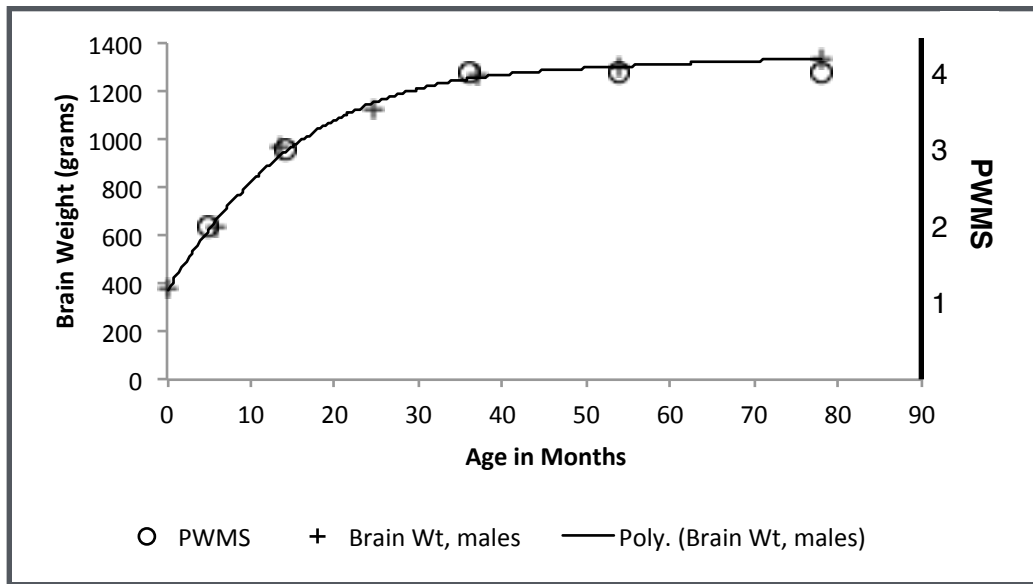


Figure 1: Change in brain weight (“+”) with age for human males compared to change in PWMS (“O”). PWMS is assumed to reach its maximum by 36 months of age when rapid growth in brain weight ceases. A 4th degree polynomial was fit to the brain weight data to illustrate the time-trend in brain weight. For the first three data points for PWMS, the correlation between brain weight and PWMS, $r = 0.998$, is statistically significant ($p < 0.04$, $n = 3$) at the $\alpha = 5\%$ level despite the small sample size. Data on human brain weight, here and in Figure 2, from Dekaban 1978: Tables 2 and 3.

400 grams of grain weight, chimpanzees would only have $PWMS^* = 1$ at adulthood. Alternatively, if we assume that in humans the main evolutionary change in the size of PWMS has been an increase in its upper bound and not in the starting size of PWMS, then we would posit, by homology between WM^* and WM , that $PWMS^* = 1$ at birth and the growth in brain size of 231 grams between birth and chimpanzee adulthood would only add, at most 1 unit of PWMS, implying that $PWMS^* = 2$ for adult chimpanzees. In either case, $PWMS^*$ for chimpanzees would, at most, be about one-half the PWMS for humans. For chimpanzees to have the same PWMS as humans, there would have to be a much higher growth rate for $PWMS^*$ in chimpanzees per unit of added brain mass than is the case for humans, hence there must have been neotenzation of cognitive development associated with brain growth in humans, but there is no evidence for neotenzation in human cognitive development (Langer, 2005, 2006; Parker and McKinney, 1999). Thus the more plausible assumption is that for adult chimpanzees $PWMS^*$ is around 2 ± 1 in comparison to humans with $PWMS = 4 \pm 1$, which implies that limitations on chimpanzee EWMS are not simply due to the various attributes that differ between WM^* and WM , but to chimpanzees having a smaller PWMS.

Human Effective Working Memory Size > Chimpanzee Effective Working Memory Size

From the prospect of performance, there are extensive data (see Read 2008) on chimpanzees showing a qualitatively less effective working memory size than is the case for humans. These

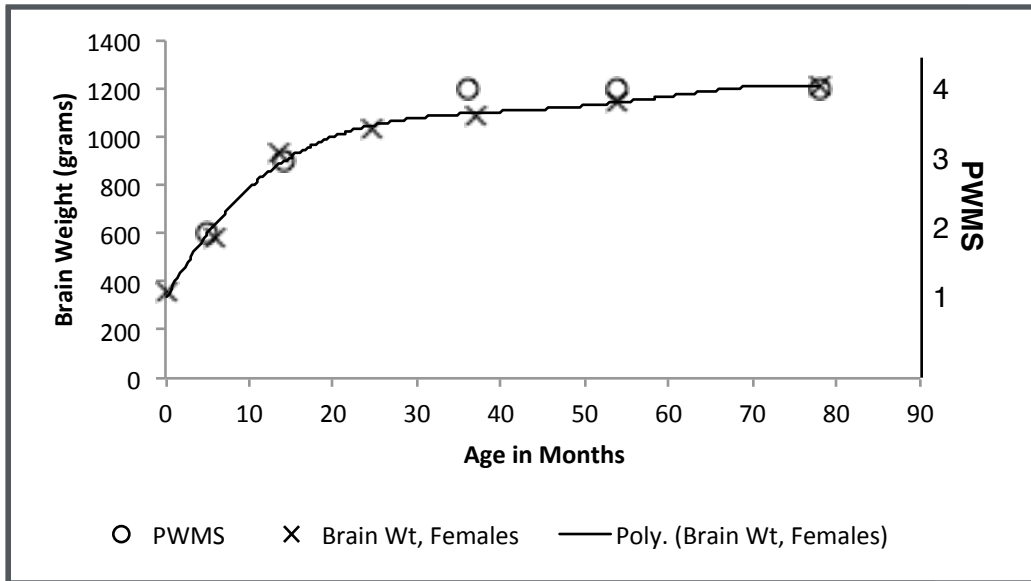


Figure 2: Change in brain weight (“+”) with age for human females compared to change in PWMS (“O”). PWMS is assume to reach its maximum by 36 months of age when rapid growth in brain weight ceases. The curve fit to brain weight is a 4th degree polynomial and is shown only to illustrate the trend in brain weight. For the first three data points for PWMS, the correlation between brain weight and PWMS, $r = 0.990$, is statistically significant ($p < 0.09$, $n = 3$) at the $\alpha = 10\%$ level.

data strongly suggest that $EWMS^* = 2 \pm 1$ for chimpanzees. Carruthers only considers one observation regarding the limits on $EWMS^*$ for chimpanzees and rejects it, as we will see in (1) below, for spurious reasons.

- (1) Perhaps the strongest evidence for the small size of the effective working memory for chimpanzees is the inability of 25% of the chimpanzees in the Taï National Park in Côte D’Ivoire, to perform a three-part sequence required for cracking nuts, despite watching, day-in and day-out, other chimpanzees do the task successfully (see references in Read 2008). The task requires selecting a stone anvil, putting a nut on the anvil, then hitting the nut on the anvil with a stone used like a hammer. We can characterize the sequence by (anvil, nut, hammer). It is reported that 25% of the chimpanzees never learn to do this sequence. They either do (anvil, nut) and hit the nut on the anvil with a fist, meaning that they just conceptualize the (anvil nut) part of the sequence, or put the nut on the ground and hit the nut with a stone, meaning that they conceptualize just the (nut, hammer) part of the sequence. In other words, though these chimpanzees desire the nut meat, and even though they see other chimpanzees do the sequence (anvil, nut, hammer), they cannot replicate the sequence despite extensive trials and repeated observations of other chimpanzees doing this sequence. Carruthers wants to dismiss this evidence by saying that it can be explained by "lack of understanding of physical forces and their effects" (p. 10373). But his statement simply describes what a chimpanzee that fails to crack a nut apparently does not understand, not the reason for failing to

understand, such as not being able to consider the sequence (anvil, nut, hammer) simultaneously in working memory.

The matter is much simpler, though, than whether chimpanzees can, or do, develop mental physics models. Enacting the sequence (anvil, nut, hammer) does not require a causal physics model on the part of the chimpanzee, but just sufficient short term memory to be able to repeat what one sees others doing. (While understanding the physical, causal connections among the anvil, nut and hammer that make it possible to achieve the goal of obtaining nut meats may be part of the cognitive/mental repertoire of the chimpanzees that successfully crack open nuts, sequences of actions may be imitated precisely even when, factually, there are no causal connections, such as ritual sequences aimed at affecting the performance of [nonexistent] gods or other spirits.) The simplest explanation for the 25% that fail to repeat the full sequence is that they have an EWMS* = 2 and cannot hold in mind, simultaneously, the elements in the sequence (anvil, nut, hammer) (see discussion and references in Read 2008). When the sequence that must be kept in short term memory is reduced to two elements due to the use of exposed tree roots as fixed anvils, as occurs with nut-cracking in Bossou, Guinea (see discussion in Read 2008), all chimpanzees are able to correctly crack nuts (McGrew *et al.* 1997). The “physical forces and their effects” that must be understood is the same in both situations: a nut must first be placed on an anvil, then the nut is struck by a rock hammer. If success in cracking nuts successfully requires first understanding the physics involved, as suggested by Carruthers, then we would have a new problem, namely why all the chimpanzees in Bossou can formulate such a model but 25% of the chimpanzees in Taï National Park cannot. A simpler and more parsimonious explanation is that the bottleneck lies in the magnitude of EWMS*, not the degree of understanding by chimpanzees of the physics involved in the process of nutcracking.

- (2) The chimpanzee Ai, in recall tests, shows at most an effective working memory of size 2. The claim by Kawai and Matsuzuwa (2000a, b) that she recalls five items, hence has a working memory size of 5, ignores the fact that in the experiment with Ai, the first item she had to identify did not involve recall, the 5th item was a forced choice (since it was the last item), and her performance on the 4th item was no better than chance, so at most she recalls 2 items (see discussion and references in Read 2008; see also Read 2008 for reasons why the more recent claim about the supposedly large size of the working memory of one subject chimpanzee is not valid — the subject chimpanzee had undergone extensive practice and was drawing on “eidetic imagery” [Inoue and Matsuzuwa, 2007, p. R1005], not working memory, and humans with similar practice outperform chimpanzees [Cook and Wilson 2010]). Carruthers mentions these data on the chimpanzees and also dismisses the claim of a large size for working memory, noting that the chimpanzee performance reflects sensory short term memory, not working memory.
- (3) Experiments aimed at introducing nut cracking into a group of naive chimpanzees also find that about 25% do not learn to crack nuts (see discussion and references in Read 2008);

- (4) In unstructured experiments allowing for free association of objects, chimpanzees manipulate one or two objects, but not three or more; this contrasts sharply with the performance of human infants (see discussion and references in Read 2008);
- (5) in various domains where simultaneous manipulation of three or more objects is possible, any instance of simultaneous manipulation of three or more objects is rare (see references in Read 2008), and even in situations where the bonobo chimpanzee Kanzi supposedly achieves linguistic functionality by simultaneous manipulation of more than a single token, the drop-off in the frequency with which he manipulates two or three tokens is still the same as occurs with other chimpanzees when comparing the frequency with which they manipulate 1, 2 or 3 objects. In other words, whatever linguistic meaning combinations of two, and rarely three, tokens may have for Kanzi, this does not translate into increased frequency of making supposedly meaningful combination of two or three tokens, which contrasts sharply with the performance of human infants as they learn a language (see discussion and references in Read 2008);

and

- (6) data on social interaction among chimpanzee infants, in sharp contrast with human infants, indicate that social interaction involving three or more active individuals does not occur with chimpanzee infants (see discussion and references in Read 2008).

While these data, with the exception of (1), can be critiqued as not directly testing the effective size of working memory (let alone PWMS*), they all point in the same direction: chimpanzees do not engage in actions, activities, or the like that would easily be possible if $EWMS^* = EWMS$ or $PWMS^* = PWMS$, all other things being kept constant.

Finally, just as for pure working memory, developmental data contradict the claim that $EWMS^* = EWMS$ for chimpanzees. Published data (see references in Read 2008) show that the size of human effective working memory begins increasing linearly with age starting at 7 months and reaches its peak around the age of puberty. The claim that $EWMS^* = EWMS$ (or that $PWMS = PWMS^*$) requires chimpanzees to develop the same working memory after 80 months as do humans after 144 months, but neotenization of cognitive development does not characterize humans (Langer, 2005, 2006; Parker and McKinney, 1999). Absent any evidence of neotenization in human memory development, we can conservatively assume the development velocity for WM in chimpanzees is the same as for humans, which implies that chimpanzees would have an effective working memory size of 2 at 42 months (and $PWMS^*$ would also be 2) when they first begin to learn how to do nut cracking, if at all.

Conclusion

In sum, the claim that $PWMS^* = PWMS$ is not supported by the evidence provided and would require a neotenized cognitive development trajectory for humans, in comparison to chimpanzees

for which there is no evidence. In addition, extensive data that relate to the magnitude of EWMS* for chimpanzees (taking into account the fact that the data are often indirect measures of EWMS*) consistently shows $EWMS^* = 2 \pm 1$, which is consistent with $PWMS^* = 2$. Finally, the evolutionary trajectory from a common ancestor to the chimpanzees and humans, beginning with $EWMS^* = 2 \pm 1$ and ending with *Homo sapiens* and $EWMS = 7 \pm 1$, fits remarkably well with paleoanthropological data on changes in hominin cognition as measured by changes in the design complexity of artifacts (Read and van der Leeuw 2008; Overmann *et al.* 2012). Indeed, recursion, one of the key aspects for the power of human cognition, does not leave traces of its inclusion in the cognitive repertoire of our ancestors until, at the earliest, the advent of the Levallois flake technology that began about 100,000 - 200,000 BP (Hoffecker 2007). Attributing the advent of recursion to secondary aspects of WM, as Carruthers must, is hardly a parsimonious account of the developmental increase of both $PWMS^*$ and $EWMS^*$ to the size that we find in modern *Homo sapiens*. Instead, a more parsimonious account recognizes that, although working memory in chimpanzees and humans are homologous, there are quantitative differences that have led to qualitative differences as evidenced by the development of cultural systems dependent upon a much more complex cognitive system than is found in the chimpanzees (Read 2012), a development that was made possible by expansion in the size of both pure and effective working memory.

Acknowledgement: I thank Peter Carruthers for a thoughtful critique of an earlier version of this article that led to elaboration, in this version of the article, on the developmental sequence for the size of pure memory and on whether subitizing is involved in the performance by Rhesus monkeys in the Hauser *et al.* 2000 experiment. Any errors in that elaboration or elsewhere in the article are solely my responsibility.

References

- Botvinick, M. M., J. Wang, E. Cowan, S. Roy, C. Bastianen, J. Patrick Mayo, and J. C. Houk. 2009. An analysis of immediate serial recall performance in a macaque. *Animal Cognition* 12(5): 671–678.
- Carruthers, P. 2013. Evolution of working memory. *Proceedings of the National Academy of Sciences USA* 110 (suppl. 2): 10371–10378.
- Chapais, B. 2008. *Primeval kinship: How pair-bonding gave birth to human societies*. Cambridge: Harvard University Press.
- Cook, P. and M. Wilson. 2010. Do young chimpanzees have extraordinary working memory? *Psychonomic Bulletin and Review* 2010 17(4): 599-600.
- Cowan N. 2001. The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences* 24: 87–185.
- _____. 2010. The magical mystery four: How is working memory capacity limited, and why? *Current Directions in Psychological Science* 19(1): 51–57.
- Cutini, S. and M. Bonato. 2012. Subitizing and visual short-term memory in human and non-human species: a common shared system? *Frontiers in Psychology* 3: 469-473.

- Dekaban, A. S. 1978. Changes in brain weights during the span of human life: Relation of brain weights to body heights and body weights. *Annals of Neurology* 4: 345-356.
- DeSilva, J. and J. Lesnik. 2006. Chimpanzee neonatal brain size: Implications for brain growth in *Homo erectus*. *Journal of Human Evolution* 51: 207-212.
- Elmore, L. C., W. J. Ma, J. F. Magnotti, K. J. Leising, A. D. Passaro, J. S. Katz, and A. A. Wright. 2011. Visual short term memory compared in Rhesus monkeys and humans. *Current Biology* 21: 975-979.
- Feigenson, L. 2007. Continuity of format and computation in short-term memory development. In M. Oakes & P. J. Bauer (Eds.), *Short- and long-term memory in infancy: Taking the first steps towards memory* (pp. 51-74). New York: Oxford University Press.
- _____. and Carey, S. 2005. On the limits of infants' quantification of small object arrays. *Cognition* 97: 295-313.
- _____. and J. Halberda. 2003. Infants chunk object arrays into sets of individuals. *Cognition* 91: 173-190.
- von Glasersfeld, E. 1982. Subitizing: The role of figural patterns in the development of numerical concepts. *Archives de Psychologie* 50: 191-218.
- Hanus, D. and J. Call. 2007. Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): The effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology* 121(3): 241-249.
- Hauser M. D., S. Carey, and L. B. Hauser. 2000. Spontaneous number representation in semi free-ranging rhesus monkeys. *Proceeding in Biological Science* 267(1445): 829-833.
- Hoffecker, J. E. 2007. Representation and recursion in the archaeological record. *Journal of Archaeological Method and Theory* 14: 359-387.
- Inoue, S. and T. Matsuzawa. 2007. Working memory of numerals in chimpanzees. *Current Biology* 17: R1004-R1005.
- Kawai, N., and T. Matsuzawa. 2000a. "Magical number 5" in a chimpanzee. *Behavioral and Brain Sciences* 24: 127-128.
- _____. 2000b. Numerical memory span in a chimpanzee. *Nature* 403: 39-40.
- Kaldy, Z. and A. M. Leslie. (2003). Individuation of objects in 9-month-old infants: Integrating "what" and "where" information. *Developmental Science* 6(3): 360-373.
- Langer, J. 2005. The primate phylogeny of cognitive ontogeny. In J. Valsiner (Ed.), *Heinz Werner and developmental science* (pp. 307-319). Berlin: Springer.
- _____. 2006. The heterochronic evolution of primate cognitive development. *Biological Theory* 1: 41-43.
- McGrew, W. C., R. M. Ham, L. J. T. White, C. E. G. Tutin, and M. Fernandez. 1997. Why don't chimpanzees in Gabon crack nuts? *International Journal of Primatology* 18: 353-374.
- Miller, G. A. 1956. The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review* 63(2): 81-97.
- Moher, M., A. S. Tuerka, and L. Feigenson. 2012. Seven-month-old infants chunk items in memory. *Experimental Child Psychology* 112(4): 361-377.
- Overmann, K. A., F. L. Coolidge, and T. Wynn. 2012. The evolution of working memory. In T. JP. Alloway & F. G. Alloway (Eds.), *Working memory: The connected intelligence* (pp. 37-40). New York: Psychology Press.

- Pagano, S., L. Lombardi, and V. Mazza. 2014. Brain dynamics of attention and working memory engagement in subitizing. *Brain Research* 1543: 244-252.
- Parker, S. T. and M. L. McKinney. 1999. *The evolution of cognitive development in monkeys, apes, and humans*. Baltimore: The Johns Hopkins University Press.
- Piazza, M. 2010. Neurocognitive start-up tools for symbolic number representations. *Trends in Cognitive Sciences* 14(2): 542-551.
- Read, D. 2008. Working memory: A cognitive limit to non-human primate recursive thinking prior to hominid evolution. *Evolutionary Psychology* 6: 676–714.
- _____. 2012. *How culture makes us human: Primate evolution and the formation of human societies*. Walnut Creek: Left Coast Press.
- _____. and S. van der Leeuw. 2008. Biology is only part of the story ... *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 363: 1959-1968.
- Reznick, J. S., J. D. Morrow, B. D. Goldman, and J. Snyder. 2004. The onset of working memory in infants. *Infancy* 6(1): 145-154.
- Simmering, V. R. and S. Perone. 2013. Working memory capacity as a dynamic process. *Frontiers in Psychology* 3: 567. doi: 10.3389/fpsyg.2012.00567.
- Tsetlin, M. M., S. I. Novikova, E. V. Orekhova, N. P. Pushina, E. V. Malakhovskaya, A. I. Filatov, and T. A. Stroganova. 2012. Developmental continuity in the capacity of working memory from infancy to preschool age. *Neuroscience and Behavioral Physiology* 42(7): 692-699.
- Wynn, T. 2002. Archaeology and cognitive evolution. *Behavioral and Brain Sciences* 25: 389-438.