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

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Abstract

In a recent article, it is argued that the pure working memory in humans and the chimpanzees are homologous with the same parameter values for the size of pure working memory. However, the data offered to support this claim show the opposite, namely that the pure working size of chimpanzees is smaller than that of humans. In addition, extensive data show that the effective size of working memory in the chimpanzees is much smaller than in humans. Altogether, there are qualitative differences between the chimpanzees and humans deriving from quantitative differences in the size of their working memory (pure or effective).

Introduction

In a recent article, Peter Carruthers (2013) argues that working memory in humans and in non-human primates are homologous 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 humans and non-human primates with respect to working memory then lies, he suggests, with the ability to resist interference when doing a task, the employment of extensive imagination, the capacity to mentally rehearse action, and so on. While these are interesting aspects of the differences between humans and non-human primate working memory, and while he has provided a useful summary of results that have been obtained regarding working memory in non-human primates, lacking in his story is how this accounts for the documented changes that took place in the cognitive capacity of the hominin ancestors of *Homo sapiens* that make us radically different than what is possible among the non-human primates. Carruthers attributes the difference to content: "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 non-human animals and implies erroneously 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 inherit in [this scenario] .... There is something else at play: an ability to construct and carry out increasingly elaborate plans of action" (p. 38). Missing in Carruthers' account is a

way to account for this remarkable difference in the cognitive ability of humans and their hominin ancestors and how this relates to differences in working memory capacities, not just to content, and underlies the qualitative differences in cognitive abilities in our hominin ancestry in comparison to the non-human primates 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).

Homology Between Human and Non-Human Working Memory

Carruther's main conclusion, 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 is constrained by the same parameters, is not justified by the evidence he presents and is contradicted by published evidence that he does not cite. He notes that his conclusion leads to the paradox that WM* is supposedly the same as WM, yet non-human primates perform qualitatively less well; however, he does not seem to consider this a problem for his story.

That working memory in humans evolved out of working memory for an ancestor of an extant great ape species — generally assumed to be the ancestor to *Pan troglodytes*, and *Pan paniscus* (Chapais 2008) —, hence chimpanzees and humans have homologous and not analogous working memory systems, is hardly controversial. The point at issue is not whether WM is evolutionarily homologous to WM*, but his claim that working memory in the non-human primates and in humans have the same parameter values for the size of working memory.

Carruthers frames his argument by using an ordinal 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 does not make sense. It is possible that (size of WM*) < (size of WM), yet otherwise WM and WM* are homologous and share all other attributes in his sequence if the primary evolutionary change in WM* going from an ancestor to the chimpanzees to humans mainly involves the size of short term memory associated with working memory. Thus Carruther's Level 2: size of WM* < size of WM, is a dimension orthogonal to his ordinal scale formed by adding additional qualitative attributes to working memory until he reaches Level 9 with no differences in WM between the great apes and humans.

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). Carruthers refers to the latter as pure working memory size, but that is a bit of a misnomer since the distinction is between hardware capacity and how that hardware capacity is implemented. Another, useful way of considering the processing-related size of working memory is as a measure of the effective size of working memory. I will distinguish between these two

measures, then, by referring to the former as the *effective working memory size* (EWMS) and the latter (following Carruthers, to avoid introducing yet another term) as the *pure working memory size* (PWMS).

The distinction is important since PWMS is, roughly, the equivalent of 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 effective performance as measured by EWMS. The same PWMS may lead to different effective working memory sizes. For our purposes here, we are concerned primarily with effective working memory size since one of the critical concerns when comparing humans 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, we also need to distinguish between non-human primates and humans when referring to EWMS. Notationally, we will use EWMS* (PWMS*) when referring to non-human primates and EWMS (PWMS) when referring to humans. The essence of Carruthers argument, then, is that PWMS* = PWMS but EWMS* < EWMS, largely for reasons relating to differences in content due to differences in verbal ability.

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

Now consider the evidence marshaled by Carruthers. The two data sets referenced by Carruthers do not validate his claim that PWMS* = PWMS.

(1) Carruthers refers to "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, but then he 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, Carruthers 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 on 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) Carruthers then refers to an experiment (Hauser *et al*. 2000) that supposedly is "not so easily critiqued" (p. 10373) as the previous experiment. 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 between 3 and 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). In other words, Carruthers assumes (but the experimenters do not) that the size of pure working memory accounts for the performance of the Rhesus monkeys. However, their

performance is an example of the wide-spread phenomenon in animal species of subitizing (see Piazza 2010 for a recent review), whereby comparison of sizes of collections up to 3 or 4 items, but not larger size collections, 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 procedure (von Glasersfeld 1982).

If it were the case that subtilizing correlated strongly with PWMS, then whether the Rhesus monkeys were making the comparison through subtilizing or by some other means would not be critical. Though it has been suggested (Cutini and Bonato 2012) that subitizing may relate to visual short term memory (in humans, visual short term memory is of size 4 and humans easily subitize collections up to size 4), this does not account for subitizing by the Rhesus monkeys as their visual short term memory is about 1/2 the size of the visual short term memory for humans (Elmore *et al*. 2011: Fig 2A), hence they should only be able to subitize collections of size 1 or 2 if the size of visual short term memory is the basis for subitizing. Consequently, the performance of the Rhesus monkeys is not driven by comparison based on the content of working memory, but by subitizing. Thus, contrary to Carruthers claim, the experiment by Hauser *et al*. showing the subtilizing ability of Rhesus monkeys is not a measure of the size of their PWMS*.

Another problem with the claim that PWMS = PWMS* is the fact that the size of PWMS is part of the developmental trajectory in humans (Cowan 2001) (and presumably in non-human primates), rather than a property in place from birth or infancy. Chimpanzees reach puberty around a calendrical age of 5 - 6 years, or at about 1/2 the calendrical age for human puberty. Were it the case that chimpanzee PWMS* = PWMS, then the velocity for the development of PWMS in chimpanzees would need to be twice that of humans, implying neotenization of cognitive development in humans for which there is no evidence (Langer, 2005, 2006; Parker and McKinney, 1999). Thus the more plausible assumption is that chimpanzee PWMS is around 2 ± 1, which implies that limitations on chimpanzee EWMS is not simply due to the various attributes that Carruthers finds are different between EM* and EM, but to chimpanzees having a fundamentally smaller PWMS.

Size of Human Effective Working Memory > Size of Chimpanzee Effective Working Memory

From the prospective 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, but not discussed by Carruthers. These data strongly suggest that EWMS* = 2 ± 1 for chimpanzee. Carruthers only considers one observation regarding the limits on the size of EWMS* for chimpanzees and rejects it, as we will see 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 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 understand and 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) — which also suggests, though not discussed by him, a limited size for EWMS*. But that statement describes, at best, why a chimpanzee that fails to crack a nut does not work out the physical cause for the failure. 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 requires sufficient memory to be able to imitate what one sees others doing. 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 sequence (anvil, nut, hammer) (see discussion and references in Read 2008);

(2) The chimpanzee Ai, in recall tests, shows at most an effective working memory of size 2. The claim that she recalls five items (mentioned by Carruthers) 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 Matsuzawa, 2007a, p. R1005], not working memory; humans with similar practice outperform chimpanzees [Cook and Wilson 2010]).

(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 objects is still the same as oc-

curs with other chimpanzees when comparing the frequency with which they manipulate 1, 2 or 3 objects; in other words, whatever linguistic understanding combinations of two, and rarely three, tokens may have for Kanzi, it 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.

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 of size 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 that Carruthers provides and would require a neotenized cognitive development trajectory for humans, in comparison it chimpanzees, for which there is no evidence. In addition, extensive data that relates to the size of EWMS* for chimpanzees (taking into account the fact that the data are often indirect measures of EWMS*) consistently shows EWMS* = 2 ± 1, which is consisted with PWMS* = 2. Finally, the evolutionary trajectory from a common ancestor to the chimpanzees, beginning with EWMS* 2 ± 1 and ending with *Homo sapiens* and EWMS = 7 ± 1, fits remarkably well with paleoanthropological data as a measure of changes in hominin cognition through changes in the design complexity of artifacts (Read and van der Leeuw 2008; Overmann *et al*. 2012). Indeed, recursion, one of the key aspects of the power of human cognitions, does not show up as part of the cognitive repertoire of our ancestors until, at the earliest, the advent of the Levallois flake

technology that begins 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 development 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 is homologous, there are quantitative difference that have led to qualitative differences evidenced by the development of cultural systems dependent upon a much more complex cognitive system than is found in the chimpanzees (Read 2012) and was made possible by expansion in the size of both pure and effective working memory.

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