On some statistical and cerebral aspects of the limits of working memory capacity in anthropoid primates, with particular reference to *Pan* and *Homo,* and their significance for human evolution

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A B S T R A C T

Some comparative ontogenetic data imply that effective working-memory capacity develops in ways that are independent of brain size in humans. These are interpreted better from neuroscientific considerations about the continuing development of neuronal architecture in adolescents and young adults, than from one about gross brain mass which already is reached in childhood. By contrast, working-memory capacity in *Pan* never develops beyond that of three- or four-year-old children. The phylogenetic divergence begs the question of whether it is any longer plausible to infer from the fossil record, that over the past two million years, an ostensibly gradual increase in endocranial volumes, assigned to the genus *Homo,* can be correlated in a scientifically-meaningful manner with the gradual evolution of our effective executive working memory. It is argued that whereas *Pan's* effective working-memory capacity is relatively similar to that of its storage working-memory, our working memory is relatively larger with deeper executive control.

1. Introduction

1.1. Working memory

The term working memory (hereinafter WM) refers to a brain system that provides us with temporary short-term storage and management of perceptual or other information (including that held in brain systems for our long-term memories), which we need for efficiently, and at high speed, carrying out, and updating, such complex cognitive tasks as mental reading (mind reading, 'Theory of Mind'), reasoning, forecasting, manipulation (e.g., playing on a piano a tune unknown to you that you hear someone singing), mental arithmetic, learning, and communication (when it is required to retain long strings of words: for instance, in German when the main verb arrives at the end of a sentence and resolves uncertainty). As Baddeley and Hitch (1974) explained, WM holds information temporarily for mental operation. The ability or capacity of WM is measurable by tests and experiments to evaluate its *size*

(WMs)[1]. A high score might correspond to a hearer being able recite in correct order the last three words of each of the last three sentences uttered together by a speaker. Experiments with apes and monkeys evaluate their ability to resolve puzzles involving the appropriate manipulation of objects to obtain a reward of desirable food or drink.

1.2. Working memory and human technological and cultural complexity

It is widely acknowledged that WM plays a fundamental role when navigating the technical and social challenges that any Primate faces in its environment. Its functional integrity is critical for achieving an adequate cognitive performance, which explains that the psychological instruments intended to measure general intelligence in humans include tasks for evaluating WM (e.g., Digit Span backward test, Corsi Block-tapping test, etc.). It has been proposed that recent evolutionary changes in the storage capacity of WM, or perhaps other evolved changes in cerebral neurobiology, could account for the complex

technologies and sophisticated cultural norms and practices that permeate human societies (Coolidge and Wynn, 2001; Hodgson, 2012; Manrique et al., 2021; Manrique and Walker, 2017; Read and Van der Leeuw, 2008; Read et al., 2009; Van der Leeuw et al., 2009; Wynn, 2002; Wynn and Coolidge, 2004). If this latter argument is correct, qualitative differences in cognitive abilities related to WM capacity, including recursive reasoning (Read, 2008; cf., Corballis, 2011), would explain why other animal species, including our closest living Primate relatives, do not display the same level of technical and social intricacy in their constructed econiches.

1.3. Scarcity of direct studies that measure WM in our closest living primate relatives

Despite the alleged importance that has been placed on WM in order to explain human evolution, there exists a lack of consensus as to how WM in great apes compares to that of humans. Interpretations of empirical evidence sometimes involve non-parsimonious inferences. Thus, although some controlled experiments have given rise to findings from which claims have been made that chimpanzees are endowed with remarkable WM abilities for storage (Carruthers, 2013; Inoue and Matsuzawa, 2007; Kawai and Matsuzawa, 2000) and updating (Völter et al., 2019), these claims are in direct conflict with other results and analytical implications published by several other researchers (e.g., Lind et al., 2023; Read, 2008; Washburn et al., 2007). In order to make a comprehensive, unbiased assessment of the WM of great apes, we conducted a critical review (see Read et al., 2022) in which we examined not only the appropriateness of methods that have been used to measure WM in nonhuman taxa of the order Primates (LINNAEUS, 1758), with special emphasis on chimpanzees, but we also reviewed the parsimony of the inferences derived from the data; that is, whether claims that were made derived directly from, or are supported sufficiently, by published data. This endeavor proved to be far more challenging than we had anticipated due to a lack of research that provides comparable measures of WM for humans and great apes. Two exceptions to this pattern of non-comparable measures of WM are the experiments conducted by Inoue and Matsuzawa (2007) and Völter et al. (2019) but, as discussed in Read et al. (2022), their experimental observations contradict the interpretations they make of their experiments. Another exception to non-comparability of WM measures for humans in relation to great apes is the experiment reported on by Lind et al. (2023). They show that even when a comparable measure of WM is used for both the great apes and humans, it is still the case that, unlike humans, the "non- human great apes … lack a memory for stimulus sequences" (p. 1). They conclude: "This may be an ability that sets humans apart from other animals and could be one reason behind the origin of human culture" (p. 1). Lastly, the experiments conducted by Washburn et al. (2007) are also an exception to the pattern of non-comparability of WM measures. Like the Lind et al. experiments, the Washburn et al. experiments show a much lower performance level for the great apes in comparison to the humans in the visuospatial tasks administered by them.

We overcame this difficulty by turning our attention (see Read et al., 2022) to some published studies of Simiform Primates that can be analyzed from the perspective of WM computational demands, albeit not having been designed for that purpose. In reaching our conclusions, we made use of Beaman's (2010) proposal for three subsystems that contribute to WM, namely:

(1) a *holding* sub-system for WM (HWM) of sensory buffers for temporary storage of rapidly decaying information undergoing manipulation;

(2) a *strategic* sub-system of WM (SWM) for enabling the establishment of goals and sub-goals for guidance of behavior that involves "hierarchical processes controlling the order in which a sequence of operations is performed (Miller et al., 1960:16)" (Beaman, 2010, S27); and

(3) an *attentional* sub-system in WM (AWM) that allows attention to be focused on significant features of one's surroundings (Cowan, 1988, 1995, 1999, 2008; D'Esposito and Postle, 2015; Morey and Cowan, 2018; Rhodes and Cowan, 2018) while filtering out distractors.

This tripartite conceptual approach enabled the identification and scrutiny of enough selected studies from which inferences could be drawn that seem to be widely applicable to WM in the great apes, as Table 1 indicates (for further information about the experiments listed in Table 1, how they were conducted, and their strengths and limitations, see Read et al., 2022).

1.4. Differences between human and chimpanzee WM sizes

A principal finding of our previous review (Read et al., 2022) had to do mainly with the holding WM subsystem, that is, the size of working memory (WMs). We came to the conclusion that far from supporting claims that human WM is equalled by that of *Pan,* the size of working memory of *Pan* is WMs = 2 ± 1, which is *below* human WMs, but also, of crucial importance, that *Pan* lacks the marked difference that is found in humans between storage-specific, "*pure*" WMs (PWMs ≥ 4 ± 1 [Cowan, 2001, 2010]), and the *executive* or *effective* WMs (EWMs, e.g., an oft-cited human WM capacity of $7 ± 2^2$ [Miller, G.A., 1956]). Appreciation of this difference suggests the plausibility of a relationship between the evolution of human behaviour and the evolution of aspects of cerebral neurobiology involved, ontogenetically, in the development of human WM in immature individuals.

EWMs is attainable by deploying mnemonic strategies, such as subvocal rehearsal or mental re-arrangement of material for recall through evolved refinement of WM into sub-systems. As mentioned above, one of these must be storage-specific WM (Cowan's "*pure*" WM, hereinafter PWM), that can well be regarded as a *holding* WM sub-system (Read et al., 2022). Another, which probably should be distinguished from "*pure*" WM (Read et al., 2022), is a *strategic* WM sub-system that guides behaviour (cf., Miller, G.A., et al., 1960). Last, but certainly not least, a third WM sub-system undoubtedly involves *attention* that in the order Primates is particularly noteworthy (cf., Bruner and Colom, 2022; Cowan, 1988, 1995; Cowan et al., 2005, 2006; D'Esposito and Postle, 2015; Fuster, 1995, esp. pp.212–236; Majerus et al., 2016, 2018; Morey and Cowan, 2018; Murray et al., 2017, esp. pp. 292–295; Passingham and Wise, 2012, esp. pp. 248–254, 330–331; Rhodes and Cowan, 2018). An evolutionary process of WM refinement could imply that, perhaps in step with evolving cerebral architecture in the genus *Homo*, WM capacity increased from WMs ≈ 4, whether measured by PWMs or by EWMs, to WMs ≈ 7 with PWMs = 4 and EWMs increasing to 7 (in *Homo sapiens* today). Executive control of WM seems to have taken a unique evolutionary course in *Homo,* resulting in qualitative and quantitative differences in cognitive capacity in comparison to all other living Primates. Plausibly, various Late Miocene and Pliocene Hominidae had a WMs of 2 ± 1, including those Hominini ancestral to *Pan, Australopithecus*, and *Homo*. (Box 1 provides readers with the acronyms used by us.).

1.5. Emergence of human WM

Early australopithecine endocrania reflect patterns of cerebral sulci more like those of great apes than those reflected in most endocrania assigned to *Homo* from around 1.5 Ma onwards. However, fossil evidence assigned to the genus *Homo* is reported from 2.8 Ma (million years ago) at the close of the Pliocene, shortly before the onset (2.6 Ma) of the Early Pleistocene, and indubitably exists by 2 Ma; de Sousa et al. (2023) remark that "*the sulcal pattern in later australopiths and early* Homo *is still debated,*" and cite Ponce de León et al. (2021). It has been argued that the rapid rate of pre- and early post-natal cerebral enlargement in *Homo* may have been absent in australopithecines who perhaps shared the

Table 1
Selection of experiments in nonhuman Simiform Primates whose data inform us about efficiency of the three WM subsystems.

Experiment	Task	Publication	WM subsystem involved	Author's interpretation	Comment
Battery of cognitive tests	Earlier age to pass the cognitive tasks	Herrmann et al. (2007);Wobber et al. (2014)	SWM, AWM	Chimpanzees perform less well in the SWM and ATM subsystems than humans and have shorter cognitive development time	
Nut-cracking	Tool-making and usage	Matsuzawa (1994)	HWM, SWM	None	Data show HWM $= 2 \pm 1$
Floating peanut	Innovating solution	Hanus et al. (2011)	SWM, AWM	Chimpanzees match human cognitive ability of human 7-year-olds	Chimpanzee average group performance comparable to human 3.5-year-olds
Memorize order of digits	Digit recall	Kawai and Matsuzawa (2000);Inoue and Matsuzawa (2007)	HWM	Chimpanzee HWM > human HWM	Data for average group performance actually show HWM $= 2 \pm 1$ for chimpanzees
Locating hidden food	Search for food in closed boxes without repeating any box, updating information is the key to success	Völter et al. (2019)	HWM, SWM	Chimpanzees have a remarkable updating WM ability	Data for average group performance actually show HWM $= 2 \pm 1$ for chimpanzees.
Rotating paddles	Planning ability	Tecwyn et al. (2013)	SWM	Limited planning abilities	
Anticipated need	Select or make tool in anticipation of future need	Mulcahy and Call (2006);Bräuer and Call (2015)	SWM	Act in accordance with future needs	Data actually show limited ability to make choices in anticipation of future need
Level-1 visual perspective taking	Follow human gaze as a function of previous experience with goggles	Karg et al. (2015)	AWM	Apes has level-1 visual perspective taking abilities	In exp. 1 apes failed to follow gaze as a function of their own previous visual experience with goggle-like masks. In a modified presentation (exp. 2) designed to hone competitiveness performance was above chance, yet still with modest (circa 60%) success.
Transparent versus Opaque Screen	Attribute mental states that one has experienced to others	Kano et al. (2019)	AWM	Apes take into account the visual perspective of competitor (Theory of Mind)	The null hypothesis that apes search where the object was previously located cannot be rejected
Visuospace working memory storage capacity	Humans, Chimpanzees, Orangutans, and Rhesus monkeys required to match from 2 to 6 pairs of images hidden on several cards lying face-down	Washburn et al. (2007)	HWM	Chimpanzees performed slightly better than at a chance with 2 or 3 pairs of images, their performance decreased to a chance level with 4 pairs of images	Data show HWM $= 2 \pm 1$ for chimpanzees
Sequencing stimuli in time	Remembering the temporal series of two successive stimuli (e.g., pictures of two common objects appearing contiguously in time on a screen) and using it to predict reward presentation	Lind et al. (2023)	AMW, HWM	Bonobos performance remains close to a chance level	

slower rate that characterises chimpanzees (Leigh, 2012). Between 2 and 1.5 Ma *Homo*, with a WMs likely approaching 4, became the prevailing genus in the formal taxonomical sub-tribe of Hominina (homininans)[3].

The evolution of an ontogenetic difference could well have enabled not only the cerebral neurobiological evolution in the homininan lineage from which *Homo* emerged of a considerable short-term memory capacity with which the effective or executive control of WM could

engage, but also the foundation of that qualitative difference in reasoning capability, vis-à-vis extant paninans[3], which prioritises *inferential* thinking about the *causes* of whatever was seen, touched, smelt, tasted, felt, or heard, such that, in *Homo*, primordial humans could learn from them about how, in accordance with successful outcomes or otherwise, they might modify their behavior differentially by varying their respective planned responses or strategies. Significant relevant circumstantial evidence is provided by the presence from 1.75 Ma of the

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Box 1

List of concepts more frequently used for easy of consultation.

WM= working memory; WMs= working memory size; HWM= holding working memory subsystem; SWM= Strategic working memory subsystem; AWM= attentional working memory subsystem; PWMs= pure working memory size in humans; EWMs= effective working memory size in humans;.

*PWMs= pure working memory size in nonhuman Primates; *EWMs= effective working memory size in nonhuman Primates.

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manual technique of the bifacial flaking of stone hand-axes and cleavers which puts complex demands on WM (Manrique and Walker, 2017).

1.6. Pure and effective WM

In order to avoid conflating the expressions PWMs and EWMs in humans with putative WMs values in plausibly homologous systems of, extant non-human species of Primates, the usage will be followed here of Read et al. (2022) who, in order to distinguish non-human PWMs and EWMs from human PWMs and EWMs, qualified writing WMs in non-human Primates as *PWMs and *EWMs. There is also a practical difficulty in evaluating PWMs and EWMs differentially in animals, which may be insuperable if the experimental design omits safeguards against possible resort by the animals to mnemonic strategies such as rehearsal or chunking. The qualifications *PWMs and *EWMs are in order, because critical scrutiny (Read et al., 2022) of the published literature has rebutted claims that WMs values $> 2 \pm 1$ have been demonstrated beyond doubt in some behavioural responses by *Pan*. This rebuttal validates the reasonable inference that ordinarily in Panini *PWMs ≈ *EWMs ≈ 2 ± 1.

2. WM size and cognitive performance: the ≤ 2 to ≥ 3 cognitive shift

Cognitive ability is limited by WM capacity. Here is a simple example. With EWMs = 2, when WM is initiated with A and B the executive function of WM can determine if A is similar to B on the basis of similar or different features and the answer to that comparison may be the basis for action; e.g., if A is an unfamiliar kind of animal but A shares features with a dangerous carnivore, the resulting action may be to flee from A. What cannot be done is to predicate the comparison of A to B on context C, where context C may affect whether the action is to flee or not; e.g., if the context is one in which A cannot get access to the acting individual, then the decision may be to not flee from A when in context C. Reasoning dependent on activating the minimum of a 3-place predicate is impossible with PWMs = EWMs ≤ 2. Only with PWMs = EWMs $\geq$ 3 (especially with EWMs > 4) is *causal* reasoning likely. PWMs = EWMs ≥ 3 is essential for unfolding qualitatively complex cognitive computations, such as recursion, analogical reasoning, strategical planning, or attribution of beliefs (Read et al., 2022; Read, 2008). In children, a transition from relying on PWMs = EWMs ≤ 2 to regularly using PWMs = EWMs ≥ 3 happens around age six. It is seen in a study (Hochmann et al., 2017) of their ages when they abandon use of 'entropy' (i.e., abandon reliance on perceptual differences expressible with 2-place predicates) and, instead, start using the abstract categories of *same* and *different* in order to solve a relational matching-to-sample task: in this study, some 3-year-olds, and most 4- and 5-year-olds, solved it based on perceptual variability between sample and target. One-third of the 5-year-olds solved it for smaller 'entropy' differences (i.e., lesser perceptual variability) and self-reported as having based their choices on the distinction between being *same* or *different,* though only 6-year-olds showed robust, successful performance (>80% success) by relying mostly on relational aspects of the task, namely the conceptual distinction between *same* and *different.* 6-year-olds are at a

developmental age when their PWMs = EWMs ≥ 3 (see Fig. 1A, Read et al., 2022). In all relational analogical problems, the two (or more) domains, events, or matters being compared must be kept temporarily active in WM together with rules or benchmarks useful for comparative purposes. These are probably lacking with PWMs = EWMs = 2 and only present with PWMs = EWMs ≥ 3.

3. Brain size need not predict cognitive performance for all ranges of WMs; furthermore, the same WMs can translate into marked differences in performance

Why is it, then, that *Pan* seems unable to act like humans (or like a Turing machine) and increase the 'performative' capacity of a *PWMs $\approx 2 \pm 1$ in order to make it work as though it had *EWMs $\approx 3 \pm 1$? Is it not puzzling that in *Pan* *PWMs ≈ *EWMs? The simplest answer is that *Pan* lacks the brain architecture that enables its 'metaphorical Central Processing Unit'[4] to act as if it has more than 3 registers, whereas human adult brains, with 4 registers, have architecture that enables them to act as if they are endowed with 7 registers. What do we mean by *Pan* lacking the architecture to amplify its WM capacity? Can its WM capacity be investigated in the laboratory?

3.1. WMs and brain size did not evolve in lockstep in Homo

Plausibly, an increase from PWMs ~ 4 to EWMs ~ 7 involved refinement of WM sub-systems of the genus *Homo* in step with evolving cerebral architecture during the Pleistocene. An evolutionary process of neuronal reorganisation that achieved the requisite cerebral architecture probably bore no particular statistical relationship to the size of adult *Homo* brains; their sizes, however, were constrained by the physical dimensions of crania. Failure to acknowledge that neither the size of human brains nor the quantity of cerebral neurones inside them is a reliable indicator of intelligence underlies a widespread notion, albeit ill-conceived (Gould, 1981 and 1986), that voluminous calvariae imply above-average cognitive abilities of their erstwhile cerebral contents. Extinct taxa of *Homo* with small adult brains negotiated formidable geographical barriers or physical obstacles: e.g., *Homo erectus georgicus* had crossed the Lesser Caucasus mountains by 1.75 Ma in the Early Pleistocene, *Homo naledi* lay inside the nowadays almost impenetrable, pitch-black, Rising Star Cave in the Middle Pleistocene, and *Homo floresiensis* had crossed the open sea to reach Flores by the Late Pleistocene. Adult cranial volume (which reflects cerebral volume) had a range of variation in early *Homo* which not only exceeded that in australopithecine homininans, but also increased over Pleistocene time (well-illustrated in Tobias, 1991, Table 181, p. 708; Fig.49, p. 709; Fig. 50, p.710), and in neither case is allometric evolution an adequate explanation. Relaxation of selection pressure could have been involved that enabled ethological and behavioral buffering of a wider range of variation in cerebral mass and endocranial volume in *Homo*, than that of chimpanzees and australopithecines, which perhaps became established genetically in our genus through evolution of epigenetic modifications of gene expression (see also Gómez-Robles et al., 2015; Sherwood and Gómez-Robles, 2017; Gunz, 2015).
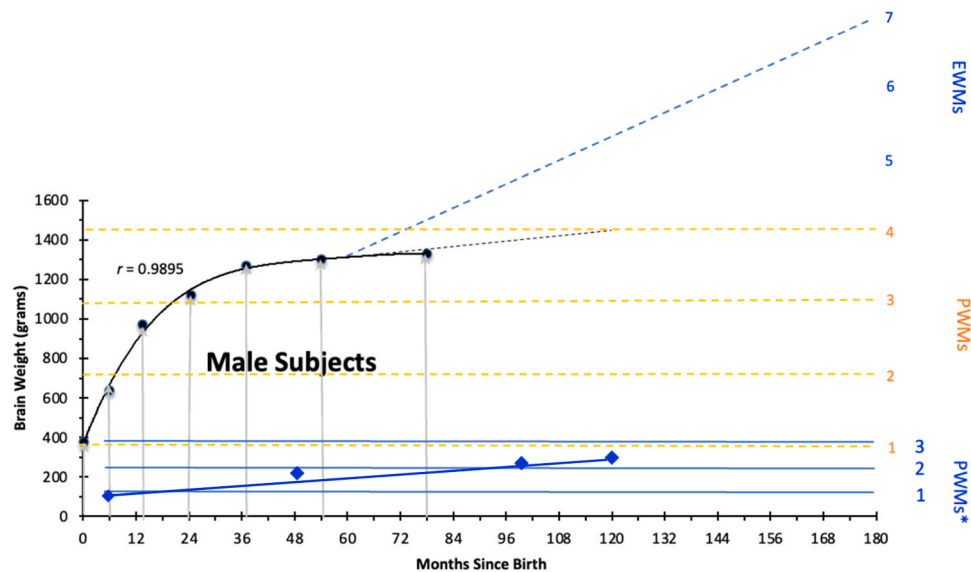
Fig. 1. Changes in brain weight and Pure and Executive Working Memory as a function of age in Pan and Homo.

3.2. Brain size and WM in humans

Large human crania are disadvantageous in so far as they can provoke obstructed labor with ensuing foetal and maternal death, and often may have done so in early *Homo*, notwithstanding evolutionary modification of the female pelvic cavity by natural selection during the Pleistocene. In human adults today, large skulls or brains do not correlate positively with memory, even if some may do so with intelligence or rapid information-processing (Tisserand et al., 2001), though published correlations with intelligence are modest at best (0.40: Wickett et al., 1994; 0.51: Andreasen et al., 1993; Gould, 1981 and 1996, esp. Chapter 3), some of which, moreover, may be due to selective sampling (Peters, 1993; Skoyles, 1999). Furthermore, psychometrical and intelligence tests are often "biased toward measuring those skills which can be measured in terms of performance against time" whilst showing "very moderate to zero correlations with people's ability to acquire expertise" (Skoyles, 1999) and thus often fail to capture those aspects of intelligence accruing in long-term WM for development of skillful expertise (Ericsson and Lehmann, 1996), which likely were of existential relevance in Pleistocene hunter-gatherer strategies. Unusual exploratory behavior could be due to a mere two or three individuals being endowed with an EWMs ≥ 3 and a competent strategic sub-system of WM.

They need not have had the largest brains. It is well-known that people with congenitally small brains, including some well-known people (e.g., Nobel laureate Anatole France, 1844–1924), have remarkable achievements to their credit (Ross, 2006; Skoyles, 1999) and there are well-documented cases of congenital microcephalic adults with I.Q. ≥ 100, including a mathematically-competent woman with I. Q. $= 112$ (Rossi et al., 1987) whose brain was around 740–760 cm^3 (Skoyles, 1999). Microcephalic adults have had careers in entertainment (e.g., 'Zip the Pinhead'; 'Schlitzie'; 'Beetlejuice'). Neurosurgeons have documented some patients who after hemispherectomy went on fulfil professional careers and had normal WM despite cerebral volumes < 800 cm^3. Although adult men have brains often up to 10% larger than women's, this is not reflected in differences in men's and women's WM size. Adult human EWMs does not vary linearly with cerebral mass. A unique aspect of the human brain is that our cerebellum occupies a relatively larger proportion of it than it does in great apes. It is involved in our working memory (Tomlinson et al., 2014) and plays a definitive role in our learning how to predict timing in a sequence of events accurately by performing computations that are fundamental in both motor and cognitive domains; its vast number of neurons and complex

connectivity with other parts of the brain mean that our cerebellum acts like a computer (Eccles, 1973; Eccles, Ito and Szentágothai, 1967), able to analyse discontinuous temporal matters with accuracy and precision (Bareš et al., 2019), and the computer analogy has inspired interesting simulations with artificial neural networks by several workers (e.g., Yamakazi and Tanaka, 2005; Furushi and Yamakazi, 2017). Meta-analyses (Yaple et al., 2019) of functional magnetic resonance imaging findings in young, middle-aged, and elderly adults, engaged in n-back WM tasks, highlight the concordance of parietal, cingulate, insular, claustral, and cerebellar cortical activity in all three groups, whereas the concordant prefrontal activity of young adults is less noticeable in middle age and absent in the elderly.

3.3. Heterochrony in human brain growth

As children grow, white matter increases somewhat more in boys than in girls, and between 10 and 12 years of age frontal and parietal gray matter increase, slightly earlier in girls than boys, before decreasing in both after adolescence (Lenroot and Giedd, 2010). Not until both are 16–17 years old does their temporal gray matter reach its maximal size (Lenroot and Giedd, 2010), which then is slightly greater in men than in women (Lenroot and Giedd, 2010). These heterochronic developments within our brains are in contrast to developmental synchrony within brains for other non-human anthropoid Primates (Giedd et al., 1999). This is likely to be of relevance to the singular evolution of human WM.

Several neuroimaging studies correlate important aspects of memory with medial temporal (including hippocampal) cortical activity in humans and other mammals, though frontal and parietal lobes are involved with memory, particularly in coordinating perceptual sensorimotor responses with WM. Longitudinal neuroimaging studies of the human brain (Giedd et al., 1996, 1999; Lange et al., 1997; Lenroot and Giedd, 2006) throw light on the development of WM between birth and adulthood. Adult human WM capacity is positively correlated with the increasing prominence in human brains between ages 6 and 25 of white-matter fronto-parietal and fronto-striatal tracts between gray-matter areas (Darki and Klingberg, 2015). WM is associated with white-matter integrity related to genetically-determined dopaminergic activity (Li et al., 2022, and references therein). White-matter tracts develop when oligodendrocytes produce fatty-acid sheaths around neuronal axons and thereby not only reduce both the leakage of ions through cell membranes and the capacitance of cell membranes, but also increase speed of nerve impulses along axons. In humans, an outcome of

the development of prominent white-matter tracts is the increasing enhancement of intracerebral connectivity, which is a particular characteristic of young people between ages 12 and 30 (Dennis et al., 2013) and peaks during late adolescence (Mills et al., 2016). It begins in childhood: white-matter connectivity in 8-year-old children, studied by magnetic resonance neuroimaging, showed positive correlation with cognitive performance (Raja et al., 2022). It has long been known that myelination develops neither at an invariant rate nor uniformly throughout the growing brain of children and teen-agers (Flechsig, 1920). It plays a minor role in babies' brains, though, even before term, its specific microstructure is detectable in the fetal brain (Gilmore et al., 2018; Lebenberg et al., 2019) and embryonic future white-matter increases almost fourfold between gestational weeks 13–20 with the appearance in week 29 of myelinated tracts (Teffer and Semendeferi, 2012). White-matter tracts may have become important in early *Homo* prefrontal cortex (Sherwood et al., 2005; Teffer and Semendeferi, 2012), with consequent enhancement of WM, plausibly facilitated by evolution of neuroanatomical and neurophysiological transmissibility of signals back and forth between anterior and caudal cerebral regions, and likely involving also cerebellar and subcortical regions of the brain.

Neuroimaging shows 20-day-old babies' brains to have a volume already about one-third of adult volumes. Gray-matter increase is mostly responsible for the increase in brain size to four-fifths of maximum volume at eighteen months (Groeschel et al., 2010), whereas, afterwards, myelinated white-matter increases steadily into early adulthood (Gilmore et al., 2018). Diffusion tensor imaging and tractography in infants under 2 years old reveal associations (Short et al., 2013) between their visuo-spatial WM and white-matter tracts connecting brain regions that support WM in older children (genu, anterior and superior thalamic radiations, anterior cingulum, arcuate fasciculus, and the temporo-parietal region). Our prefrontal cortex supports cognition and integration of WM in executive control of behavior. A neuroimaging study (Matsui et al., 2016) of its gray and white matter, in 107 individuals aged between 1 month and 25 years old, found that older children and young adolescents had more dorsolateral prefrontal cortex gray matter than infants and adults, that dorsolateral prefrontal cortex white-matter volumes in children and both young and older adolescents were larger than infants', and that dorsomedial prefrontal cortex white-matter volumes of young and older adolescents, as well as adults, were larger than infants' (the different age groups showed little difference with regard to the orbitofrontal cortex). From the aforementioned findings, two stages of dorsal prefrontal cortical change were inferred: the first being characterized by growth spurts of both gray and white matter before 2 years of age, and the second by changes in gray-matter volume in older children and young adolescents. Interestingly, the maximal development of gray matter in children's frontal cortex is not reached until they are 11 - 12 years old, whereas elsewhere in the brain it is reached between 6 and 9 years of age (Teffer and Semendeferi, 2012). Teffer and Semendeferi (2012, p. 194) commented that "The development of the prefrontal cortex is characterized by growth in early childhood, decrease in adolescence, and then a slight increase and stabilization in adulthood. This pattern is thought to be linked to the maturation of cortical circuits that underlie frontal lobe functioning, including language, decision-making, attention control, and working memory" and (p.196) "The dorsolateral PFC, a region involved in executive functioning, begins to lose gray matter only at the end of adolescence. Reduction in gray matter volume continues in the frontal lobe until adulthood and is most pronounced in adolescence and early adulthood (Sowell et al., 1999)" (PFC = prefrontal cortex).

3.4. WM and the growing brain: white matter matters

WM involves the superior dorsolateral prefrontal cortex where neuroscientific research on macaques detects neuronal activation seemingly associated with mnemonic introspection for spatial meta-recognition and a self-monitoring ability to recognize accuracy (Kwok

et al., 2019)[5]. Myelination of white-matter tracts continues beyond late adolescence in young people, at least up to age 25 (Bethlehem et al., 2022; Groeschel et al., 2010; Miller et al., 2012; Sherwood and Gómez-Robles, 2017; Sowell et al., 1999). By contrast, myelination is complete in white-matter tracts of pubertal macaques, and, although perhaps incomplete in pubertal chimpanzees (Sakai et al., 2010, 2011, 2012, 2013), myelination is complete when they are sexually mature (Miller et al., 2012). The life-span of rhesus macaques often exceeds 25 years, but they may show cognitive decline from as early as 12 years of age (Moore et al., 2006) in mid-life when also a reduction in white matter is detectable in dorsolateral prefrontal cortex and frontal, and anterior cingulate cortices of the monkeys (Dash et al., 2023; Kohama et al., 2012). Unlike them, protracted immaturity increasingly has defined the trajectory of cerebral evolution in *Homo* (Semendeferi and Hanson, 2016), and Coward (2012) suggested that prolongation during human ontogeny of an increase in cerebral white matter represents a significant phylogenetically evolved characteristic of our genus. De-myelination of neuronal axons and reduction in white matter are detected quite frequently in brains of middle-aged humans (Fotenos et al., 2005; Moher et al., 2012) who may or may not proceed to show cognitive impairment (perhaps implying a reduction in both EWMs and executive control); by and large, intracortical myelin in the human brain seems to be associated with unimpaired performance and cognitive aptitude (Grydeland et al., 2013).

Examples of the importance of the human prefrontal cortex for WM include activity in dorsolateral prefrontal cortex when we hold rules in memory which influence performance of tasks involving ventral prefrontal cortex and "frontopolar" anterior prefrontal cortex (Bengtsson et al., 2009). When rules are in conflict, dorsolateral prefrontal cortex governs behavioral modification (Boschin et al., 2017), whilst dorsomedial prefrontal cortex monitors evaluation of self or others while undertaking tasks (Piva et al., 2019). Research on monkeys indicates superior dorsolateral prefrontal cortex engagement with mnemonic introspection for spatial meta-recognition and self-monitoring ability to recognize accuracy (Kwok et al., 2019), implying WM involvement, whereas ventromedial prefrontal cortex is concerned with comparison, choosing, and deciding (Papageorgiou et al., 2019), and inferior ventrolateral prefrontal cortex with retrieval of episodic memory (Anderson et al., 2007). Rapid learning about the value of novel behavior especially involves frontopolar prefrontal cortex (Boschin et al., 2015; cf. Qiu et al., 2018) that plays a fundamental part where performance of WM tasks takes time and when salient impingements require remedial attention with novel behavioral responses (Boschin and Buckley, 2015), or possibly where prior induction underpins planning (e.g., "What is a likely outcome if I do such-and-such?") or where incongruous or counterfactual conjectures are brought to mind that respond to meta-cognitive reflexion (e.g., "What were to have happened to us if the sun had not risen?" "What would be the outcome were a malign force to try to thwart my doing such-and-such?" "What if I were to die while trying to do it?"). From the standpoint of the evolution of human cognition, it is significant that our frontopolar prefrontal cortex is absolutely larger than great-ape frontopolar prefrontal cortex, and, moreover, occupies a relatively larger proportion of frontal cortex (Teffer and Semendeferi, 2012).

Findings from studies of neuronal activity in human brains indicate associations between WM and activity in occipital and temporal cortices, between WM content and activity in ventrolateral prefrontal cortex and parieto-occipital cortices (Quentin et al., 2019), and between salient impingements and activity in hippocampal cortex, dorsolateral prefrontal cortex, and the medial orbitofrontal cortex which seems to be involved especially when impingements are anticipated (Jafarpour et al., 2019). Orbitofrontal cortex neurons appear to play a part in executive control, both in setting a task and in restoring control over an ongoing task after a mistake or error has occurred, which implies a capacity to monitor the state of executive control in relation to mnemonic information about likely outcomes of behavior based on experience,

while maintenance of control is supported by dorsolateral prefrontal cortex and the anterior cingulate cortex (Mansouri et al., 2022). In anthropoid Primates, a noteworthy aspect related to WM is the ability to focus and maintain attention on intricate tasks, and neurobiological research on rhesus monkey brains points toward the existence of an attentional "hub" in their ventrolateral prefrontal cortex (Kadohisa et al., 2023). Time-consuming tasks to which humans attend can place heavy demands on executive control and may require postponement of gratification for many hours or days, with complex feed-back and feed-forward between short- and long-term memory, not only with regard to WM but also to procedural, episodic, semantic, constructive, and prospective mnemonic processes. It is relevant to point out here that endocraniological research indicates that early *Homo* at 2 Ma had frontal lobes that were still ape-like in several respects, and that only by 1.5 Ma, in the young "Turkana Boy" *Homo erectus*, do they foreshadow their modern human configuration (Ponce de León et al., 2021).

Perhaps our teenagers' mental agility and enhanced WM owe much to heterochronic extension beyond childhood of neuronal coactivity between prefrontal and caudal cerebral regions during evolution of *Homo*. The prolongation is limited, however. Thus, a neuroimaging study of a memory task (Finn et al., 2010) found that whereas prefrontal and hippocampal cortices were co-active during WM in 15-year-old girls undertaking a task, the coactivity was absent in WM when they undertook the task at 18 years old. A neuroimaging study involving arithmetic tasks showed that between ages 7 and 9, children perform less counting and increasingly more memory-based numeric retrieval, accompanied by increased hippocampal functional connectivity at the expense of the previously predominant prefrontal-parietal WM system (Qin et al., 2014), implying increasing development of aspects associated with our mature WM that is characterized by EWMs ≈ 7. Perhaps the increases owe to the continuing strengthening of executive control over effective WM (EWM) in children *after* PWMs ≈ 4 has been reached at an age of about 4 years. Using functional connectivity, a neuroimaging study of the memory of scenes observed by children, adolescents, and young adults (Tang et al., 2018) showed that with their increasing age there was an increase in functional connectivity between prefrontal cortex (dorsolateral and ventrolateral prefrontal cortices) and medial temporal cortex during the formation of memories, and part of the increase was due to negative effects recorded in superior and medial prefrontal cortex that indicate differential involvement of prefrontal regions in supporting memory formation. As other neuroimaging studies have demonstrated, memory-formation involves ventrolateral prefrontal cortex and medial temporal cortices. Nevertheless, WM is widely distributed in the brain (Christophel et al., 2017; Fuster, 2001, 2015), which renders difficult our attempts to reconstruct the evolution of WM in erstwhile brains that occupied fossil skulls of *Homo*. Our modern brains hold out few hints and many snares. Thus, Lenroot and Giedd (2006, p. 726) pointed out that "Total brain size is 95% of maximum size by age 6, although cortical and subcortical components of the brain change dramatically during childhood and adolescence" and "…the amount of plasticity present in even the adult brain has also made clear that the relationship between factors affecting brain development and the resultant brain structures is staggeringly complex… the structure of the brain at any time is a product of interactions between genetic, epigenetic, and environmental factors."

4. "Pure" working memory size in infants and young children: a base-line for considering evolution of WM in *Homo*

Notwithstanding the lack of any obvious positive correlation between neuronal elements that contribute, on the one hand, to PWMs, and, on the other hand, to cerebral mass, weight, volume, or architecture, and despite problems of formulating the relation of endocranial dimensions to cerebral mass, weight, volume, or architecture, it is informative, nevertheless, to reflect on whether some aspects of a not implausible, hypothetical, evolutionary development of the genus *Homo*, from a homininan precursor with PWMs = EWMs = 2 ± 1, into

early phylogenetic forms of *Homo* with PWMs = EWMs ≥ 3, and then into *Homo* with PWMs = 4 and EWMs > 4. This evolutionary pattern might stand, perhaps, in a confirmable statistical relationship to inferences drawn not only from cranial and other evidence relevant to cerebral evolution in Hominini, Hominina, and *Homo*, but also from consideration of WMs identifiable at different ontogenetic stages, from fetus to mature adulthood, of *Homo sapiens* nowadays.

Let us consider this last possibility first. Active WM is detectable undoubtedly in 5.5-month-old babies (Reznick et al., 2004), though between 4 - 5 and 6.5 - 7 months they seem able to detect change only in a one-item array but not in arrays of two or three items, consistent with PWMs = 1 (Feigenson, 2007; Káldy and Leslie, 2003; Kibbe and Leslie, 2013; Ross-Sheehy et al., 2003; see also Oakes and Luck, 2013; Simmering, 2012; Zosh and Feigenson, 2015), and at 7 months a qualified limit of PWMs ≤ 2 was proposed by Moher et al. (2012), who noted that "7-month-olds fail to remember three hidden objects when no chunking cues were provided". Feigenson (2007) notes that Ross-Sheehy et al. (2003) suggest that some experiments showing 5-month-old infants with PWMs ≈ 2 could involve long-term memory because infants were able to view objects for several seconds rather than the 500 ms for experiments with infants showing PWMs = 1. Thus, the data show that for the 4 - 6.5 months age-range, PWMs ≈ 1, and at 7 months PWMs ≤ 2 at most. What is beyond doubt is that infants in the 4 - 7 months age-range do <u>not</u> show PWMs = 3. By 8–9 months, infants can focus attention on 3 items, but do not individuate them: "However, infants and young children would not be able to use the deliberate system adequately to separate the stimulus stream into discrete events …" (Cowan, 2016, p. 248). Thus, they have not fully reached PWMs = 3 by 8–9 months of age.

By the end of the first year of infancy a noteworthy increase has taken place in visual short-term memory capacity in prefrontal cortex (Ross-Sheehy et al., 2003), which likely corresponds to neuronal developments. By 10 - 12 months, infants' PWMs ≈ 3 (Feigenson and Carey, 2005; Moher et al., 2012), showing correlation with prefrontal cortical activity (Tsetlin et al., 2012), and thereafter it increases to its final value of PWMs = 4, which is reached at around 3 years of age (or perhaps later). Thus, Cowan (2016), implying a somewhat slower rate of increase), stated that 10 – 12-month-old infants have PWMs = 3, but do <u>not</u> have PWMs = 4: "Infants [10 or 12 months old] succeeded only when one, two, or three crackers were placed in either bucket, and chose entirely by chance when required to remember larger numbers…" (Feigenson, 2007, p.58). Similarly, Kibbe and Leslie (2013) wrote that 12 – 13-month-old infants "can apparently individuate three items sometime around the end of the first year." Feigenson (2007, p. 71) concluded "These findings raise the possibility that the capacity of short-term memory increases over the first year of life…" Published data, then, show that, at most, PWMs = 3 for 12-month-old infants, but <u>no</u> data show PWMs = 4 at 12 months of age. Instead, the data point to an increase in PWMs starting as early as 4 months of age and continuing until ≥ 4 years of age to a final value of PWMs = 4. In other words, 7-month-old infants have, at most, PWMs = 2; questionably, they may have PWMs ≤ 2 at 7 months of age; 10 – 12-month-old infants have, at most, PWMs ≈ 3; and, at most, our final PWMs = 4 is reached by ≥ 4 years of age.

5. Relation between growth in white matter and expansion of EWMs

Fig. 1 shows the relationship established between brain weight and age and how these factors relate to Pure and Executive WM for *Pan* and *Homo*. Perhaps the most striking aspect of Fig. 1 is that the graph for *Homo* is not simply a scaled-up version of the graph for *Pan*. The graphs are both qualitatively and quantitatively different. Qualitatively, the increase in EWMs for *Homo* beyond PWMs = 4 has no counterpart in *Pan* since PWMs* = EWMs* for *Pan* at all ages. The relation between PWMs and Age in *Homo* is a pronounced curvilinear pattern with a rapid

growth rate for brain weight during the first 14 months after birth, then the growth rate decreases and brain weight approaches its adult value asymptotically. For *Pan*, the growth in brain weight is low and similar at all ages and so the relation between PWMs* and Age appears to be linear in *Pan*. One notable similarity between *Pan* and *Homo* is the approximate tripling of brain weight from birth to adulthood in both. However, PWMs quadruples in size in *Homo* over this time period whereas PWMs* only increases between twice and three times its initial size in *Pan*, which, like PWMs for *Homo*, is assumed to be 1 at birth.

The reported increase in PWMs during biological development in *Homo* is from PWMs = 1 at birth to PWMs = 3 by around 20 months. However, for experiments conducted with infants, the measurement of the size of WM depends on whether what is being measured is just the number of hidden objects the infant is responding to, or whether the infant must also respond to the features of the hidden objects. Not surprisingly, infants can remember a larger number of objects that have been hidden when they do not need to recall the features of the hidden objects than when they must also respond to their features (Moher et al., 2012). Thus, "younger infants appear to have a smaller working memory capacity, at least for object features (Káldy and Leslie, 2005; Kibbe and Leslie, 2011; Ross-Sheehy et al., 2003)" (Moher et al., 2012, p. 364).

Without the mnemonic device of chunking, 7-month-old infants fail the hidden object test when 3 objects have been hidden. With respect to features, 7-month-old infants "have difficulty maintaining the features of more than one item in working memory (Káldy and Leslie, 2005; Ross-Sheehy et al., 2003)" (Moher et al., 2012, p. 364). This limitation can be circumvented through chunking. Previous research shows that chunking comes into play with infants at 14 months when clues for chunking are presented to them (Feigenson and Halberda, 2004) and recent research shows that chunking can likewise occur with 7-month-old infants (Moher et al., 2012). However, this appears to be unique to *Homo* because, whilst non-human animals can also chunk, it has been pointed out by Moher et al., (2012, p. 363) that their achievement is possible "only after many hundreds of training trials" – see Terrace (1987, 1991); Terrace and Chen (1991))". In *Homo,* the chunking capacity develops between 7 and 14 months of age and goes from chunking that requires redundancy in the presentation of a cluster of various cues together in order for it to occur, to occurring after a single cue for chunking has been presented. The authors conclude that "… chunking may be a foundational computation — one used from infancy

onward" (Moher et al., 2012, p. 374).

Adult total human brain weight and PWMs each reach their maximum values in modern humans around age 80 months (Dekaban and Sadowsky, 1978: Table 2). Memory performance, though, does not cease with maximum brain weight, but continues to "increase steadily as a function of age from about 7 years through adulthood" (Cowan, 2017, p. 99). The increase in EWMs beyond its value at 80 months occurs with biological maturation rather than through increase in brain weight. Given the possibility that there may be a causal link between increase in memory performance and increase in gray matter or white matter, now consider whether gray matter or white matter (or possibly neither) has a growth pattern beyond 80 months paralleling the increase in EWMs. If it does, the brain matter whose increase parallels the increase in EWMs in *Homo* suggests that increase in EWMs to its adult value of EWMs = 7 ± 2 may be due to increase in that brain matter.

The growth pattern for gray matter in humans shows increase through childhood, then reaches a maximum in the early juvenile stage when gray matter volume begins to decrease after PWMs reaches its maximum value of 4 by about age 80 months (see Table 2). Contrast this with growth in white matter in humans. Like gray matter, white matter increases from infancy but, unlike gray matter, white matter continues to increase (though at a diminishing rate with increase in age) beyond puberty until EWMs reaches its adulthood value of 7 ± 2 (see Table 2). Thus, the growth pattern for gray matter does not match the growth pattern of EWMs for humans and is strikingly different than the growth pattern for white matter. The latter, however, has a growth pattern similar to that of EWMs. By around 80 months, when PWMs has reached its maximum value of 4 and brain weight has reached its maximum value, the gray matter volume is reducing but white matter has not yet reached its maximum volume, which suggests that it is the increase in white matter that facilitates increase in EWMs through aiding the development of mnemonic strategies such as rehearsal or chunking, each of which is known to increase the EWMs measure of WM beyond its PWMs value. It has been shown that humans begin to develop chunking strategies, possibly by late infancy, and definitely by early childhood (Stahl and Feigenson, 2014). Increase in white matter in humans enables myelination of neural circuits that facilitate brain signal transmittal, which plausibly facilitates increase in EWMs even without increase in PWMs. A recent investigation using a voxelwise approach using tract-based spatial statistics (Li et al., 2022) conducted with adult

Table 2
Changes in gray matter and white matter as a function of age.

Brain changes during growth					
WHOLE BRAIN	**Infancy**	**Childhood**	**Adolescent**	**Young Adulthood**	**Change in Mean**
	0 to 2 years old	2 to 10-12 years old	10-12 to 18 years old	18 to 24 years old	
Gray Matter	Increase	Increase	Decrease	Decrease	—
Trend:	—	6.3 years old	—	21.0 years old	-14.8%[1]
Sample Mean Age:					
White Matter	Increase	Increase	Increase	Increase	—
Trend	—	6.3 years old	—	21.0 years old	+ 33.2%[1]
Sample Mean Age:					
PREFRONTAL	4.0 years old	—	—	30.0 years old	-23% to − 32%[3, 4]
Gray Matter Cortex	—	6.3 years old—	—	21.0 years old	-16.7%[1]
Sample Mean Age				11.5 years old[2]	
FRONTAL				12.5 years old[1]	
Gray Matter					
Age at Maximum Volume:					
Lobe					
Cortex					
White Matter	—	6.3 years old	—	21.0 years old	+ 30.1%[1]
Cortex					
Sample Mean Age					

1. Matsui et al. (2016).
2. Giedd et al. (1999).

3. Pfefferbaum et al. (1994).
4. Reiss et al. (1996).

humans (aged 25 to 80) showed associations between white-matter-WM over multiple white-matter tracts, which reinforces the idea of WM being a widely distributed resource (Christophel et al., 2017), one requiring dynamic agile communication across multiple brain regions.

Cowan (2017) suggests that measuring working memory during child development from infancy through childhood is complicated by two aspects of working memory that develop differently. One is the number of files that provide the storage location for the information inserted into temporary memory. An active file signifies the presence of an object stored in memory. The other complication is the extensiveness of the feature information about objects that is stored in those files. The number of active files relates to the number of objects stored in working memory regardless of whether feature information is stored as well. Also, feature information may be stored but not retrieved and the extensiveness of stored feature information can range from the sparse information stored by infants to juveniles with their extensive feature information for an object stored in a file. Cowan suggests that an infant already may have 2 or 3 files and the number of files only increases with growth slowly, if at all. What increases, he suggests, is the extensiveness of the stored information relating to object features. Thus, if what the experiment measures is the number of objects that a subject can recall from memory, this value may be found to be close to its adult value, even with infants, whereas if what the experiment measures is the number of objects for which the subject has stored feature information and can recall object features correctly from memory, the measured WM value will begin around 1 and increase quickly and asymptotically with age towards its asymptotic value of 4 (see Fig. 1). In other words, for Cowan, what increases with cortex growth is not the number of files but the cognitive ability to expand, recall, and coordinate the range of information about objects that is stored in WM. In like vein, Ma et al., 2014 regard WM as a "limited resource… distributed flexibly among all items to be maintained in memory…. the quality rather than the quantity of working memory representations determines performance" (Ma et al., 2014, p. 347). All of this requires efficient and accurate brain communication and the expansion of white matter may aid in that task, hence would lead to an increase in EWMs.

Now let us compare the growth pattern for gray matter and white matter in non-human Primates to that of humans. The growth and then decline in gray matter in non-human Primates is similar to that of human gray matter. White matter in the non-human Primates initially follows the pattern followed by gray matter, namely an increase that ceases by, and possibly before, puberty. What differs between the non-human Primates and humans is that the growth in white matter in humans, but not in the non-human Primates, continues beyond adolescence.

6. The increase in human EWMs that occurs after its PWMs reaches an asymptote represents a singular evolutionary outcome in the sub-tribe Hominina, that appears to be associated with the human characteristic adolescence growth spurt

Fig. 1 shows that Brain Weight in humans correlates curvilinearly with Age from birth to about 80 months. For this time period, PWMs = EWMs $\leq$ 4. It also indicates that EWMs and PWMs (on average) goes from EWMs = PWMs = 4 at Age = 60 months to PWMs = 4 with EWMs = 7 by Age = 180 months. We conclude that (a) children's brain volume predicts PWMs until around 8 years of age, and hence cognitive performance until around 8 years of age and, moreover, (b) that increase in WM thereafter gives rise to an effective EWMs $\approx 7\pm 2$ that is independent of brain size. On the other hand, *PWMs = *EWMs for *Pan* at all ages. This is an intriguing finding that has profound implications. For instance, changes in white matter that are presumably responsible for the increases in EWMs that occurs during late childhood and adolescence in modern humans would leave no traces in the archaeological record. This casts serious doubts regarding the reliability of measuring brain volume alone as an indicator of cognitive potential in species of humans closer to modern *Homo sapiens*. PWMs refers to the capacity

limits of WM and is equivalent to the focus of attention of WM described by Cowan (2001), the size of which is 4. There are several ways in which WM storage capacity can be expanded to an EWMs of size 7; e.g., (1) through rehearsal of the information as to when we repeat something we want to retain in memory; (2) through recoding of the information through actively seeking associations between the items to be encoded based on knowledge we have stored in long-term memory (classify objects by categories); or (3) chunking items to be recalled in more easily remembered higher-order units, for instance by forming words that make sense to us from single letters that separately are meaningless, thereby making easier to recall these letters. When using these and other mnemonic strategies the storage capacity of WM is almost doubled (PWMs = 4 becomes EWMs = 7). It is the ontogenetic developments in cerebral neuronal architecture, reflected in neuroimaging and neuro-anatomical properties, that contribute to the remarkably protracted time span for the maturation of our brain. These developments have enhanced cerebral connectivity, leading to the efficient transmission of information across neuronal systems involved with the executive control over memory throughout adolescence and into the mid-twenties of our adult life. It is reasonable to infer also that an important evolutionary change in modern human cognition is linked not only to increases in WM storage capacity but also to gains in executive control or the ability to engage with the contents of WM that boost computational efficiency.

Endnotes.

1. One of the key features defining WM is that it is a limited resource. Cowan et al. (2008) distinguish three main different types of limits that we can ascribe to WM. One refers to *temporal limits*, meaning that information in WM rapidly fades unless acted upon (i.e., unless we repeat it), the second type is *chunk capacity*, referring to an alleged space limit, e.g., when we have to put eggs into a carton and only a limited number of slots are available. The third limit can be envisaged as that of a *resource*, involving the availability of electrophysiological energy for distribution among the information to be held and stored in WM. An animated discussion has taken place over the years about the possibility of extending the capacity limits of WM, which has led authors to differentiate between pure and compound WM limits. Here, pure limits would coincide roughly with the limits (4 $\pm$ 1) of Cowan's focus of attention (Cowan, 2001) and compound limits would refer to the maximum amount of information that can be retained when the information held at the focus of attention is acted upon or rearranged (e.g., through subvocal rehearsal, or recoding of stimulus items into ever-higher order single chunks by drawing on information already stored in long-term memory). The concepts of pure and compound WM capacity estimates have been reformulated as pure (PWMs) and effective working memory sizes (EWMs) (Read, 2017), which are the terms adopted in this review. PWMs in humans would be roughly equivalent to the capacity limits of Cowan's focus of attention (4 $\pm$ 1), while EWMs would be roughly equivalent to Miller's magic number (7 $\pm$ 2).

2. Miller's (1956) 7 $\pm$ 2 is not a statistical formulation such as 'mean $\pm$ standard deviation', but instead expresses the range of values (e.g., the number of single items or chunks of psychologically meaningful units) normally observed in practice for the holding capacity of the human WM system. A more recent investigation (Gignac, 2015) that gathered data from 85 years of applying the Digit Span forward test (Ns 7.077) calculated mean $\pm$ sd values (6.56 $\pm$ 2.39) that are remarkably similar to the figures provided by Miller half a century earlier. By analogy with Miller's 7 $\pm$ 2 for *Homo*, Read (2008) introduced the expression 2 $\pm$ 1 for the WM holding capacity of *Pan* inferred from qualitative differences in nut-cracking abilities of members of the genus *Pan*.

3. Biologists assign humans and great apes to the hominid *family* of Hominidae, which is divided into the well-defined *subfamilies* of Ponginae (orangutans) and Gorillinae (gorillas), and the less homogeneous homin<u>in</u> *subfamily* of Homininae (homin<u>ins</u>: chimpanzees,

bonobos, humans). Zoologists separate the Homininae subfamily into the *tribes* Panini (chimpanzees, bonobos) and Hominini (homi*nines*). Several paleobiologists subdivide those tribes into the *subtribe* of Paninina (paninans: chimpanzees, bonobos) which are not habitual bipeds, and the subtribe Hominina (homi*nans*: *Homo sapiens* plus extinct taxa, e.g., *H. neanderthalensis*, *H. erectus*, *Australopithecus*, *Paranthropus*, etc.) of habitual bipeds. Phylogenetic separation of hominans within the Homininae began around 6 million years ago, according to inferences drawn from comparative genetic analyses and palaeontology. The genus *Homo*, evolved from bipedal australopithecine hominans, and appears in the African geological record slightly before the Pliocene epoch gave way ca. 2.58 Ma to the Pleistocene epoch and was an obligate biped by ca. 2 Ma.

4. A metaphorical analogy for the difference between PWMs and EWMs is the single register of a Turing machine (PWMs=1) that can function as if it has several registers instead of just one (EWMs>1; for further discussion of the difference between PWM and EWM, see Read et al., 2022). The EWM registers make it possible to add the number A to the number B and then be able to act on the outcome C of that addition even with PWMs= 1 by using one EWM register for A, one for B, and the one more for the outcome of A+B. The EWM registers are part of the CPU and are analogous to short-term memory and relate to the logical circuits of the CPU in much the same way that short-term memory relates to the executive functioning of working memory. "*Registers are very high-speed storage areas located inside the CPU. After CPU gets the data and instructions from the cache or RAM, the data and instructions are moved to the registers for processing. Registers are manipulated directly by the control unit of CPU during instruction execution. That is why registers are often referred to as the CPU's working memory. Since CPU uses registers for the processing of data, the number of registers in a CPU and the size of each register affect the power and speed of a CPU.*" (AWS Cloud Essential CPU Courses: CPU Registers. http://generalnote.com/Computer-Fundamental/Computer-Memory/CPU-Registers.php; accessed January 19, 2022; emphasis added). Of course, here we are making a purely metaphorical analogy, given obvious differences between the biological composition of brains and the construction of computers. Nevertheless, the analogy helps us to understand that the failure of both qualitative and quantitative cognitive performance of chimpanzees, where PWMs= *EWMs ≈ 2, to match that of humans with PWMs= 4 and EWMs ≈ 7 may be due not only to the 4 *Homo* cerebral quasi-'CPU' registers (PWMs ≈ 4) versus *PWMs= 2 for *Pan,* but also for the 4 PWM registers in *Homo* working as if they are ≈ 7 registers.

5. We must stress that the concept of working memory is separate from psychophysical evidence of cerebral mirror-neuron circuitry. Mirror-neuron circuits in monkey prefrontal cortex and parieto-temporal cortices track observed manual actions, be these performed by the monkey itself or by its handler (di Pellegrino et al., 1992; Gallese et al., 1996; Iacoboni, 2005, 2009; Iacoboni et al., 1999; Keysers and Fadiga, 2008; Nelissen et al., 2011; Papadourakis and Raos, 2018; Rizzolatti, 2005; Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2006, 2008; Rizzolatti et al., 2004). Cerebral neuroimaging shows analogous responses in humans (e.g., Shmuelof and Zohary, 2008), in parietal, frontal motor, and prefrontal cortices (Mukamel et al., 2010), as well as medial temporal cortex. Whilst neither is involved directly with memory (Caramazza et al., 2014), nor with "embodiment" of motor cognition, mirror neurons nevertheless support cognition (Kemmerer, 2014) by registering sensitivity to perceived actions of self or others. They subserve WM via perceptual-mnemonic components for computing outcomes ("goals"; cf., Umiltà et al., 2008). Monkey mirror-neuron circuits respond to transitive actions that are observed, though, in contrast to human infants, intransitive actions, mimed silently, elicit no response (Ferrari et al., 2005), from which it may be wondered whether monkey neuronal circuitry is biased by an inherent

pre-potent impediment against responding to silent mime, and whether a similar pre-potent impediment existed in human precursors, which could have diminished the contribution of mirror-neuron circuits to the evolution of human WM.

Left Side of Graph. The curve is the fit of a 4th degree polynomial to male human data on brain size and age to illustrate the curvilinear relation between Brain Weight (in grams) and Age (in months). Gray vertical arrows connect mean age of an age cohort with the mean brain weight for that cohort. The graph shows that Brain Weight correlates curvilinearly with Age (r = 0.9895; H0: ρ = 0, p < 0.001, n = 5) from birth to about 80 months. For this time period, PWMs = EWMs ≤ 4. **Right Side of Graph**. The vertical scale for PWMs (in orange) assumes PWMs varies linearly with age, as shown by the equispaced, dashed horizontal orange lines. The more extended vertical axis (with scale values in both orange and blue) is for *Homo* showing EWMs (on average) going from EWMs = PWMs = 4 for *Homo* at Age = 60 months to PWMs = 4 with EWMs = 7 by Age = 180 months. Visually, the PWMs for each age cohort almost perfectly match the fitted curve (see vertical gray arrows), thus corroborating the assumption that PWMs increases linearly with brain weight. **Lower Part of Graph.** Data for *Pan* are shown in the lower part of the graph with solid blue diamonds. *Pan*, on average, reaches *PWMs = 2 by 49 months, though individual members of *Pan* may reach *PWMs = 2 before Age = 49 months. The less extended vertical axis (right side, bottom) shows PWMs* values for *Pan* with equispaced, horizontal blue lines. For *Pan*, *EWMs = PWMs* = 3 is reached by 75% of *Pan* by 120 months and for the remaining 25% of *Pan*, *EWMs = PWMs* = 2 and never reaches *EWMs = PWMs* = 3 for individuals, even by Age = 180 months. The differences in scale between the two vertical axes is due to the much slower growth rate for brain weight in *Pan* in comparison to *Homo*. Data for modern humans were obtained from Dekaban and Sadowsky (1978: Table 2) and *Pan* data points in the lower part of the graph were obtained from Read et al. (2022).

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