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Tracing the evolutionary trajectory of verbal working memory with neuro-archaeology --Manuscript Draft--

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Abstract:	<p>We used optical neuroimaging to explore the extent of functional overlap between working memory (WM) networks involved in language and Early Stone Age toolmaking behaviors. Oldowan tool production activates two verbal WM areas, but the functions of these areas are indistinguishable from general auditory WM, suggesting that the first hominin toolmakers relied on early precursors of verbal WM to make simple flake tools. Early Acheulian toolmaking elicits activity in a region bordering on Broca's area that is involved in both visual and verbal WM tasks. The sensorimotor and mirror neurons in this area, along with enhancement of general WM capabilities around 1.8 million years ago, may have provided the scaffolding upon which a WM network dedicated to processing exclusively linguistic information could evolve. In the road map going forward, neuro-archaeologists should investigate the trajectory of WM over the course of human evolution to better understand its contribution to language origins.</p>	
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BIOGRAPHY

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4 **TRACING THE EVOLUTIONARY TRAJECTORY OF VERBAL WORKING**
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6 **MEMORY WITH NEURO-ARCHAEOLOGY**
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35 **ABSTRACT**
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37 We used optical neuroimaging to explore the extent of functional overlap between working
38 memory (WM) networks involved in language and Early Stone Age toolmaking behaviors.
39 Oldowan tool production activates two verbal WM areas, but the functions of these areas are
40 indistinguishable from general auditory WM, suggesting that the first hominin toolmakers relied
41 on early precursors of verbal WM to make simple flake tools. Early Acheulian toolmaking elicits
42 activity in a region bordering on Broca's area that is involved in both visual and verbal WM tasks.
43 The sensorimotor and mirror neurons in this area, along with enhancement of general WM
44 capabilities around 1.8 million years ago, may have provided the scaffolding upon which a WM
45 network dedicated to processing exclusively linguistic information could evolve. In the road map
46 going forward, neuro-archaeologists should investigate the trajectory of WM over the course of
47 human evolution to better understand its contribution to language origins.
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52 **INTRODUCTION**
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55 Working memory (WM) is a process that temporarily stores and manipulates
56 representations in relation to one or more goals. Multiple modalities of information are processed
57 in WM, including visual (De Benni et al., 2005), auditory (Kumar et al., 2016), tactile (Fassihi et
58 al., 2014), olfactory (Jönsson et al., 2011), gustatory (Lara et al., 2009), and linguistic (Acheson
59 and MacDonald, 2009) information. There is also brain circuitry dedicated to different
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4 subdomains; for example, object- and visuo-spatial WM activate separate ventral and dorsal neural
5 systems, respectively (Courtney et al., 1996). In this paper, we will attempt to trace the evolution
6 of verbal WM in early *Homo* using a neuro-archaeological approach, and in so doing, we hope that
7 WM may provide the bridge between praxic action and language in an evolutionary context.
8

9 The amount of verbal information that the brain can hold and manipulate in order for a
10 person to achieve a goal or solve a problem specifies the capacity of verbal WM. Verbal WM and
11 its corresponding subdomains are critical for language acquisition, subvocal rehearsal, assigning
12 syntactic structure to determine the meaning of an utterance, and remembering information during
13 a conversation (Gathercole and Baddeley, 2014). Without verbal WM, modern language as we
14 know it would not exist. Therefore, at least the base elements of verbal WM needed to be present
15 in Arbib's (2016) hypothesized "language-ready brain" for fully modern language to develop. At
16 this point, however, very little is known about the evolution of verbal WM because of the lack of
17 direct fossil evidence for cognition and language.
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19 The multicomponent model is often used to describe WM as a central executive that acts
20 as a supervisory system over two independent short-term memory buffers that store verbal
21 (phonological loop) and nonverbal (visuo-spatial sketchpad) information and an episodic buffer
22 that temporarily stores and binds multimodal information from subsidiary systems and long-term
23 memory (Baddeley, 2000; Baddeley and Hitch, 1974). How nonlinguistic auditory, tactile, and
24 other forms of sensorimotor information map onto the multicomponent model, however, is "far
25 from clearly established" (Baddeley, 2012, p. 13). For example, some studies suggest a
26 hemispheric dissociation, where the right and left PFC are engaged during visual and verbal WM
27 tasks, respectively, such as while remembering faces versus remembering names over a delay
28 (Rämä et al., 2001; Rothmayr et al., 2007).
29

30 It is unlikely that all of the listed modalities map (visual, auditory, tactile, etc.) onto the
31 multicomponent model. Therefore, it is not the ideal model for investigating the evolution of WM.
32 Rather, one more akin to Goldman-Rakic's (1996) domain specificity hypothesis might be more
33 appropriate for deciphering an evolutionary account of WM. Under this model, each specialized
34 domain is localized to a different anatomical subdivision and has its own processing and storage
35 mechanisms, which could explain why object-based visual and auditory WM pathways extend
36 from sensory regions to different parts of the frontal cortex, for example (see Kumar et al., 2016;
37 Lehnert and Zimmer, 2008). Under this model, it is possible to explore overlap between two or
38 more WM circuits as a potential indicator of common descent.
39

40 Neuroimaging and neurophysiological studies confirm that WM in human and nonhuman
41 primates involves parallel, distributed neuronal networks that manage different sensory domains
42 of information (Constantinidis and Procyk, 2004; Schulze et al., 2010). Were these WM domain
43 networks always separate from each other? Verbal WM, for example, is only found in humans and
44 is therefore a more recent evolutionary development. Did it evolve from one of these pre-existing
45 WM networks or does it reflect cultural evolution, providing a new skill to reshape existing WM
46 resources?
47

48 Perhaps neuro-archaeology can shed light on these questions. As some of the only
49 surviving artifacts for early human manual skill and cognition, stone tools are the best option
50 available for scientists to learn about past hominin brain operations at specific points in the past
51 (Stout and Hecht, 2015; Wynn, 1979). In many cases, the exact function of the tools is unknown,
52 but through many replicative studies conducted over the years, it has become increasingly clear
53 how stone tools were made (Whittaker, 1994). Therefore, neuro-archaeological research has
54 focused on the toolmaking process foremost, though there has been some pilot
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4 electroencephalography research done on prehistoric tool use (Williams et al., 2014). By using
5 neuroimaging techniques to record the brain activity of modern-day subjects as they replicate the
6 process of making stone tools, a neuro-archaeological approach pinpoints exactly which brain
7 networks are active in modern subjects, which can then be informative about the cognitive features
8 that were likely the most important for completing these toolmaking tasks at different points in the
9 past. The activation of specific neural circuits while carrying out certain prehistoric behaviors need
10 not imply that these neural circuits evolved for the purpose of these behaviors, only that these
11 circuits were likely already in place before these behaviors arose; otherwise, the behaviors in
12 question would have been impossible to perform because of a motor or cognitive limitation.

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15 Although many studies have assumed that features or objects are represented independently
16 of each other in WM, recent evidence suggests that these representations are organized in a
17 hierarchically structured fashion (Nie et al., 2017). Some researchers propose that the cognitive
18 processes (i.e., WM) involved in combining objects in a hierarchical organization and combining
19 words into sentences are homologous and occur in the same neural structure (Fadiga et al., 2009;
20 Greenfield, 1991). For example, the hierarchical thinking required to form and interpret complex
21 sentences as well as in nonverbal tasks with high WM demands activates the posterior third of the
22 inferior frontal gyrus (BA 44) known as Broca's area (Fiebach and Schubotz, 2006). Fadiga and
23 colleagues (2009) also suggest that the ventral premotor cortex (vPMC) is tuned to detect and
24 represent abstract, hierarchical structures. The hierarchical sequencing of language and the
25 technological actions involved in stone tool production, specifically Acheulian tool production,
26 are hypothesized to be the result of similar cognitive processes (Mahaney, 2014; Stout et al., 2008).
27 If this is the case, then we should be able to show that stone tool production activates Broca's area
28 and vPMC, which could be informative about the evolution of verbal WM. If, however, verbal
29 WM and stone tool production are completely unrelated cognitive processes, then it may be
30 difficult to learn anything at all about the evolution of verbal WM by monitoring the brain activity
31 associated with making stone tools.

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36 This brings up three important questions that this paper will address. First, what (if
37 anything) can neuro-archaeology conclude about the evolution of verbal WM? Second, do
38 language and toolmaking rely on the same WM network to any extent, and did they evolve along
39 a single pathway at any point during the course of human evolution? Lastly, what are further open
40 questions on how the brain got language that neuro-archaeology is prime to address in future
41 studies?
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44 **NEURO-ARCHAEOLOGICAL INSIGHTS INTO THE EVOLUTION OF** 45 **WORKING MEMORY** 46

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49 There have been some promising developments made in neuro-archaeology regarding the
50 evolution of WM that have thus far focused solely on Oldowan and Acheulian stone technologies
51 (e.g., Stout et al., 2015; see also, Stout, 2018). These stone industries appeared 2.6 and 1.75 million
52 years ago (mya), respectively (Beyene et al., 2013; Semaw et al., 1997). Oldowan technology
53 involves the expedient method of obtaining a sharp flake tool by striking a core with a hard
54 hammerstone with the knapping gesture (Toth 1985). Resulting non-standard cores reflect the
55 original shape of the stone (Fig. 1a-b). The early Acheulian technology involves a more advanced
56 form of knapping called 'alternate flaking,' which is used to thin and shape a stone into a standard
57 handaxe shape (Fig. 1c-d). Some researchers claim that the appearance of the Acheulian
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4 technocomplex in the archaeological record signifies an increase in cognitive capacity and the
5 introduction of protolanguage (e.g., Arbib 2011; Shipton 2010).
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8 (FIGURE 1 ABOUT HERE)
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10 Here we focus on a recent study that uses functional near-infrared spectroscopy (fNIRS) to
11 investigate the functional brain networks underlying Oldowan and Acheulian tool manufacture
12 (Putt et al., 2017). fNIRS is a neuroimaging technique that measures changes in cortical
13 oxygenated and deoxygenated hemoglobin and produces reconstructed images of localized
14 functional brain activity that can be directly compared to fMRI results (Wijeakumar et al., 2017).
15 Because fNIRS is less influenced by motion artifacts than fMRI, it can be used to measure real-
16 time, localized cortical activity as people make stone tools.
17

18 After completing seven training sessions, the participants' oxygenated and deoxygenated
19 hemoglobin cortical levels were measured with fNIRS while they replicated the process of
20 Oldowan and early Acheulian toolmaking. Data were collected from alternating 1-min toolmaking
21 blocks and 15-s rest periods during both of these tasks. This experiment assessed differences in
22 brain activity for an Acheulian task as contrasted with an Oldowan task and thereby focused on
23 cognition changes at one point in prehistory around 1.8 mya when early *Homo* presumably
24 innovated the more complex Acheulian industry.
25

26 This study found that Acheulian toolmaking involves the guidance and integration of visual
27 and auditory WM representations in the vPMC. The Acheulian task activates a brain network that
28 is also employed during tasks that are within the skillset of modern humans alone, such as piano-
29 playing (Bangert et al., 2006). This is likely because both tasks are complex, involving bimanual
30 coordination, the integration of multiple modes of sensory information, and goal-directed decision-
31 making based on a fixed set of affordances (i.e, number of keys on a piano versus number of angles
32 less than 90° on a core). Oldowan toolmaking, on the other hand, depends on a lateral premotor
33 system that recognizes and assigns significance to external objects based on external visual input.
34 These findings, along with the dearth of complex stone tools prior to 1.75 mya, indicate an
35 expansion in WM capabilities at this time.
36

37 Putt and colleagues (2017) assume that Acheulian toolmaking relies on a visual WM
38 network because the coordinates associated with the activated vPMC are noted in a visual WM
39 meta-analysis (Wijeakumar et al., 2015). This seems logical, as handaxe production relies on
40 constant monitoring of the intermediate steps that must be deduced before one can reach the end
41 goal state(s) (see Fig. 1c). It is unclear to what extent visual WM areas are involved in stone
42 toolmaking because of the nature of the analysis used. It focused only on the Oldowan-Acheulian
43 contrast, and the results were compared exclusively to the coordinates of known visual WM
44 centers, thus biasing the interpretation toward visual WM. Therefore, the extent that stone
45 toolmaking recruits other WM networks like verbal WM is unknown. To gain a clearer
46 understanding of the WM networks involved in stone tool production tasks, we present the results
47 of two region-of-interest analyses, which explore the relative activation of known visual and verbal
48 WM centers during stone toolmaking tasks.
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50 51 52 53 54 55 56 *Working memory centers activated during stone tool production*

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58 Did early *Homo* succeed at making complex Acheulian tools because of an evolutionary change
59 to their visual WM capacity, allowing them to store and manipulate more information than their
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4 primate predecessors? Or was this technical innovation possible because they developed a unique
5 way of thinking in the form of verbal WM? Because of the relative complexity of the Acheulian
6 toolmaking task, having even a proto-verbal WM could have been beneficial to prehistoric
7 toolmakers because they could store and process complex action sequences as simple concepts,
8 thus increasing their understanding of interrelated parts and actions.
9

10 We collected coordinates of visual and verbal WM regions-of-interest from two meta-
11 analyses, a visual WM meta-analysis that includes delayed match-to-sample and change-detection
12 tasks (Wijekumar et al., 2015) and a language-processing meta-analysis (Vigneau et al., 2011).
13 With these coordinates, we extracted values representing the level of change in the neural signal
14 in the corresponding brain space of our participants during Oldowan and Acheulian knapping tasks
15 and rest periods. Data were included from 16 participants who learned to knap without verbal
16 instructions (see Putt et al., 2017 for more information on the methods used to obtain and process
17 neuroimaging data). The knapping values were statistically compared to the rest values using a
18 Wilcoxon signed-rank test to determine if knapping significantly activated these visual and verbal
19 WM areas.
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22 Three visual WM regions were identified where the knapping signal is significantly higher
23 than the rest signal, including the left frontal eye field and dorsolateral prefrontal cortex (dlPFC)
24 in both hemispheres (see Fig. 2a). The frontal eye field forms part of a dorsal visual attention
25 network (Corbetta and Schulman, 2002) and is only significantly activated during the Oldowan
26 task. This result affirms what was found in the Oldowan-Acheulian contrast. The bilateral
27 activation of dlPFC during the Acheulian task, however, is a novel result. The dlPFC is associated
28 with a wide range of executive control functions, including planning, executing goal-directed
29 behaviors, deductive reasoning, and decision-making (Coutlee and Huettel, 2012; Heekeren et al.,
30 2006; Kaller et al., 2011). It is also one of the more important substrates for visual WM. The
31 differential activation of bilateral dlPFC between the two toolmaking tasks suggests that making
32 an Acheulian handaxe has a more ambiguous goal hierarchy and greater search depth than making
33 Oldowan tools (Kaller et al., 2011), meaning that the sequence of actions needed to make an
34 Acheulian handaxe is much less obvious. Also, Acheulian toolmaking requires mental generation
35 of sequences and evaluation of the interdependency of individual actions, while Oldowan
36 toolmaking is primarily based in visual search (see Fig. 1). These results further support three
37 claims: 1) Acheulian toolmaking is a more cognitively demanding task than Oldowan toolmaking;
38 2) complex stone tool manufacture probably relies on a visual WM network; and 3) the appearance
39 of the Acheulian industry in the archaeological record may mark a transition in the visual WM
40 capabilities of early *Homo*.
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47 (FIGURE 2 ABOUT HERE)
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49 Of the seven verbal WM regions included in the analysis, there were only two areas
50 significantly activated during the stone toolmaking tasks. These included the left dorsal pars
51 triangularis, which forms the anterior portion of Broca's area, and the right anterior middle frontal
52 gyrus, which also overlaps with the anterior dorsal part of pars triangularis (see Fig. 2b). The signal
53 in the left dorsal pars triangularis is significantly higher than the resting signal for both the
54 Oldowan and Acheulian tasks, while only the Oldowan task signal is higher than the rest signal in
55 the right anterior middle frontal gyrus. The increase in technical complexity with the advent of the
56 Acheulian industry therefore cannot be attributed to the evolution of verbal WM per se.
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4 Both of the noted areas are associated with phonological WM functions rather than
5 semantic or sentence-level processing functions (Vigneau et al., 2011). For example, the former is
6 activated in tasks that involve pseudo-word repetition (Warburton et al. 1996), word articulation
7 versus word reading (McGuire et al. 1996), and reading consonant strings (Jessen et al., 1999).
8 The function of the latter area is thought to be related to auditory selective attention without
9 specificity for language (Petit et al., 2007). While these results could be attributed to including
10 modern, language-using human subjects in the experiment or to the limited array of technologies
11 tested (considered at length in the 2018 road map below), the most likely interpretation is that the
12 activated areas are better characterized as general auditory WM centers that participate in tasks
13 involving the monitoring of both auditory and verbal stimuli.
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16 Macaques have neurons in this same cytoarchitectonic region of the ventrolateral PFC that
17 respond to complex sounds, such as animal and human vocalizations, environmental sounds, and
18 white noise (Romanski and Goldman-Rakic, 2002), indicating that the participation of this region
19 in auditory WM functions long predates its use for language functions. Combined with the
20 auditory-processing areas in the temporal lobe that come online during the Acheulian toolmaking
21 task (Putt et al., 2017), the activated areas may participate in a perception-action cycle during stone
22 tool production in which their discriminatory properties would be useful for distinguishing
23 between meaningful sounds, including sounds that are informative about successful vs.
24 unsuccessful flake removal, the size of the flake removed, and the presence of faults within the
25 material.
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29 To more explicitly inspect the amount of spatial overlap between visual and verbal WM, a
30 third analysis was conducted that involved constructing 8 mm spheres around the coordinates of
31 seven verbal WM cortical regions and eleven visual WM cortical regions from two unrelated meta-
32 analyses (Vigneau et al., 2011; Wijeakumar et al., 2015) and plotting these spheres in the same
33 brain space using Analysis of Functional NeuroImages (AFNI) software.
34

35 The results confirm that there is little overlap between verbal and visual WM centers in
36 general; however, there are two regions where they converge (see Fig. 3a). This overlap occurs at
37 the vPMC at the junction between pars opercularis and the precentral gyrus in both hemispheres,
38 overlapping with Broca's area in the left hemisphere. The left vPMC is also activated during
39 Acheulian toolmaking in the Oldowan-Acheulian contrast conducted by Putt et al. (2017) and
40 Stout et al. (2008; see Fig. 3b).
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43 (FIGURE 3 ABOUT HERE)
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46 The vPMC receives inputs from multiple sensory and association areas related to WM and
47 is thought to maintain and monitor sensorimotor information in WM to make decisions about
48 motor output (Pardo-Vazquez et al., 2011). It therefore could be an integration area where visual
49 and auditory WM join to form higher-order categories of auditory-visual events, which would
50 explain why this area is activated during WM tasks regardless of the mode of sensory information
51 being processed. The vPMC is also the site of mirror neurons, which play an important role in
52 relating perception to action (Grèzes et al., 2003).
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55 **DISCUSSION**

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58 WM is critical to language functions. Any discussion of “how the brain got language” need also
59 consider how modern WM evolved in our human ancestors. Coolidge and Wynn (2005) propose
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4 that a recent genetic mutation precipitated the evolution of an “enhanced” WM in *H. sapiens*,
5 which ushered in the modern human mind by leading to an increase in the phonological loop that
6 was later exapted by language. Language then was responsible for a form of inter-modular thinking
7 unique to humans. This hypothesis relies on Baddeley’s multicomponent model rather than a
8 domain-specific model; although, the participants in a recent workshop on this topic acknowledged
9 that we are far from distinguishing between WM as a single, nondomain-specific system or a series
10 of different kinds of WM for different kinds of problems (Wynn and Coolidge, 2010). Coolidge
11 and Wynn’s hypothesis also assumes a revolutionary scenario for the evolution of an enhanced
12 form of WM, which would imply that it is an all-or-nothing trait that individuals either possess or
13 not. This is in contrast to evidence that human WM varies within a population (Just and Carpenter,
14 1992). In the latter case, a more gradual Darwinian explanation for its evolution should be invoked
15 (Wynn and Coolidge, 2010). Nevertheless, the archaeological record indicates a rather sudden
16 cultural explosion during the Upper Paleolithic that Coolidge and Wynn use to support their
17 hypothesis for punctuated cognitive evolution. We suggest instead that the gradual evolution of
18 verbal WM networks out of previously existing structures was responsible for the ramping up of
19 cumulative culture during the late Pleistocene because of the benefits to linguistic communication
20 it instilled.

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25 The results of the region-of-interest analyses presented here, as well as previous neuro-
26 archaeological research, support that Early Stone Age toolmaking tasks recruit visual and auditory
27 WM networks, while the recruitment of verbal WM centers is dubious. The most likely
28 interpretation is that Oldowan and Acheulian toolmaking tasks employ an ancestral auditory WM
29 network that is also present in non-human primates and is sometimes incorporated into verbal WM
30 tasks in humans. In other words, auditory WM might have been an early precursor to verbal WM.
31 Additionally, there is not much overlap between visual and verbal WM regions-of-interest, which
32 indicates that language and Early Stone Age tool manufacture rely on different WM networks.
33 These results are consistent with the idea that Early Stone Age toolmaking taps evolutionarily early
34 forms of WM, while verbal WM likely evolved later than the appearance of the Acheulian industry.

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37 One point of interest however, is that the vPMC appears to be an integration area that
38 processes both verbal and visual information in WM and also becomes active during Acheulian
39 toolmaking in modern humans. Therefore, the visual and verbal WM networks are not completely
40 separate from each other, and for this reason may have shared a common evolutionary pathway at
41 one point before diverging into different networks of the brain, leaving the vPMC as a remnant of
42 this ancient network. In this scenario, vPMC served as a starting point for the evolution of verbal
43 WM because its sensorimotor integration and mirror neurons would have been indispensable for
44 complex imitation (see Arbib, 2011) and the ability to interpret the intentions of multimodal
45 communicative signals from conspecifics. Hence, vPMC may have provided the early human brain
46 a scaffold on which to build a WM that would eventually process verbal information. The fact that
47 the more complex of the two Early Stone Age tool industries tested activates not only this
48 integrative WM area but also visual and auditory WM areas could signify an advancement in WM
49 abilities around 1.8 mya that laid the foundation for the evolution of verbal WM.

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53 For there to be selective pressures on the brain to hold and process increasingly more
54 complex communicative information, there would have needed to be some form of protolanguage
55 already in place. Thus, the earliest form of protolanguage would have needed to rely solely upon
56 visual and/or auditory WM at first, similar to how modern, language-trained apes presumably
57 process linguistic information without a WM committed to verbal information. The leap to a full-
58 fledged language would not have been possible until a verbal WM network evolved that was
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4 dedicated to processing linguistic information. Once this occurred, cultures would have then
5 rapidly diversified, leading to what appears in the archaeological record as bursts of cultural
6 activity in different areas and at different points in time.
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9 **TOWARDS A NEW ROAD MAP**

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11 While WM is implicit in the specifications of complex action recognition and imitation, as of yet,
12 it is unclear what the role of WM is in Arbib's Mirror System Hypothesis. Until we have a fuller
13 understanding of the different "types" of WM that exist and how they relate to one another
14 evolutionarily, it will be difficult to specify its role in this hypothesis. Going forward, the 2018
15 road map should more explicitly consider the part that WM played in the evolution of language
16 precursors, such as complex action recognition and imitation, pantomime, and protolanguage.
17 Neuro-archaeological methodology should be further explored as a possible means to investigate
18 the trajectory of verbal WM networks over the course of hominin evolution.
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21 First we must test the hypothesis that verbal WM areas are recruited during stone
22 toolmaking tasks because of the possibility that a lifetime of language use permanently alters
23 modern human participants' functional neuroanatomy. Future studies could record the brain
24 activity of non-human primates as they make chipped stone tools to test this assertion. Bonobos
25 (*Pan paniscus*) and orangutans (*Pongo pygmaeus*) are capable of removing flakes from a core in
26 a similar manner to Oldowan tool production (Wright, 1972; Toth et al., 1993), which would offer
27 an appropriate comparison, as verbal WM areas are activated even during the Oldowan task. If
28 homologous areas are inactive in non-human primates under similar conditions, then we could
29 infer that the activation of these verbal WM areas reflects a human strategy of processing the same
30 task by using language.
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32
33 Second, we must test the hypothesis that the process of making later-occurring tools of
34 greater complexity require more extended functions of verbal WM, such as semantic and sentence-
35 level processing. To test this assertion, similar experiments should be conducted that look at the
36 extent of verbal WM involvement during the production of increasingly more complex
37 technologies that appear later in the archaeological record. For example, the cognitive abilities
38 needed to haft stone points to wooden shafts with compound adhesives during the Middle Stone
39 Age, including the capacity for multilevel operations, abstract thought, and recursion, have been
40 directly compared to the sentence-level processing of language (Wadley, 2010).
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6 **FIGURE CAPTIONS**
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8 **Fig. 1.** Goal hierarchy and production stages associated with Oldowan flaking (a-b) and early
9 Acheulian handaxe manufacture (c-d). These particular goal hierarchies reflect the thought process
10 of the first author while working toward the overarching goals of making the featured tools. Each
11 goal can only be accomplished if all of its underlying subgoals are also accomplished. The
12 Acheulian production stage (d) demonstrates how easy it is to snap a core if proper attention is not
13 directed to each of the subgoals.
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17 **Fig. 2.** Active visual WM (a) and verbal WM (b) areas during stone tool production tasks. Red
18 circles represent WM coordinates determined by meta-analyses (Wijeakumar et al., 2015 in the
19 case of visual WM and Vigneau et al., 2011 in the case of verbal WM). Only regions where the
20 signal associated with the stone tool production tasks is significantly higher than the signal
21 associated with rest periods are included. Significant Wilcoxin signed-rank tests where $p < 0.05$
22 are marked by an asterisk. Error bars in the bar plots represent 95% confidence intervals.
23 Percentage signal change is in μM units.
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27 **Fig. 3.** Ventral premotor cortex, where functional overlap occurs between visual WM and verbal
28 WM in both hemispheres (a) and Acheulian tool manufacture in the left hemisphere (Putt et al.,
29 2017) (b).
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