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TRACING THE EVOLUTIONARY TRAJECTORY OF VERBAL WORKING MEMORY WITH NEURO-ARCHAEOLOGY

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ABSTRACT

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.

INTRODUCTION

Working memory (WM) is a process that temporarily stores and manipulates representations in relation to one or more goals. Multiple modalities of information are processed in WM, including visual (De Benni et al., 2005), auditory (Kumar et al., 2016), tactile (Fassihi et al., 2014), olfactory (Jönsson et al., 2011), gustatory (Lara et al., 2009), and linguistic (Acheson and MacDonald, 2009) information. There is also brain circuitry dedicated to different subdomains; for example, object- and visuo-spatial WM activate separate ventral and dorsal neural systems, respectively (Courtney et al., 1996). In this paper, we will attempt to trace the evolution of verbal WM in early *Homo* using a neuro-archaeological approach, and in so doing, we hope that WM may provide the bridge between praxic action and language in an evolutionary context.

The amount of verbal information that the brain can hold and manipulate in order for a person to achieve a goal or solve a problem specifies the capacity of verbal WM. Verbal WM and its corresponding subdomains are critical for language acquisition, subvocal rehearsal, assigning syntactic structure to determine the meaning of an utterance, and remembering information during a conversation (Gathercole and Baddeley, 2014). Without verbal WM, modern language as we know it would not exist. Therefore, at least the base elements of verbal WM needed to be present in Arbib's (2016) hypothesized "language-ready brain" for fully modern language to develop. At this point, however, very little is known about the evolution of verbal WM because of the lack of direct fossil evidence for cognition and language.

The multicomponent model is often used to describe WM as a central executive that acts as a supervisory system over two independent short-term memory buffers that store verbal (phonological loop) and nonverbal (visuo-spatial sketchpad) information and an episodic buffer that temporarily stores and binds multimodal information from subsidiary systems and long-term memory (Baddeley, 2000; Baddeley and Hitch, 1974). How nonlinguistic auditory, tactile, and other forms of sensorimotor information map onto the multicomponent model, however, is "far from clearly established" (Baddeley, 2012, p. 13). For example, some studies suggest a hemispheric dissociation, where the right and left PFC are engaged during visual and verbal WM tasks, respectively, such as while remembering faces versus remembering names over a delay (Rämä et al., 2001; Rothmayr et al., 2007).

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

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

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

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

This brings up three important questions that this paper will address. First, what (if anything) can neuro-archaeology conclude about the evolution of verbal WM? Second, do language and toolmaking rely on the same WM network to any extent, and did they evolve along a single pathway at any point during the course of human evolution? Lastly, what are further open questions on how the brain got language that neuro-archaeology is prime to address in future studies?

NEURO-ARCHAEOLOGICAL INSIGHTS INTO THE EVOLUTION OF WORKING MEMORY

There have been some promising developments made in neuro-archaeology regarding the evolution of WM that have thus far focused solely on Oldowan and Acheulian stone technologies (e.g., Stout et al., 2015; see also, Stout, 2018). These stone industries appeared 2.6 and 1.75 million years ago (mya), respectively (Beyene et al., 2013; Semaw et al., 1997). Oldowan technology involves the expedient method of obtaining a sharp flake tool by striking a core with a hard hammerstone with the knapping gesture (Toth 1985). Resulting non-standard cores reflect the original shape of the stone (Fig. 1a-b). The early Acheulian technology involves a more advanced form of knapping called 'alternate flaking,' which is used to thin and shape a stone into a standard handaxe shape (Fig. 1c-d). Some researchers claim that the appearance of the Acheulian technocomplex in the archaeological record signifies an increase in cognitive capacity and the introduction of protolanguage (e.g., Arbib 2011; Shipton 2010).

(FIGURE 1 ABOUT HERE)

Here we focus on a recent study that uses functional near-infrared spectroscopy (fNIRS) to investigate the functional brain networks underlying Oldowan and Acheulian tool manufacture (Putt et al., 2017). fNIRS is a neuroimaging technique that measures changes in cortical oxygenated and deoxygenated hemoglobin and produces reconstructed images of localized functional brain activity that can be directly compared to fMRI results (Wijeakumar et al., 2017). Because fNIRS is less influenced by motion artifacts than fMRI, it can be used to measure real-time, localized cortical activity as people make stone tools.

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

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

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

Working memory centers activated during stone tool production

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

We collected coordinates of visual and verbal WM regions-of-interest from two meta-analyses, a visual WM meta-analysis that includes delayed match-to-sample and change-detection tasks (Wijeakumar et al., 2015) and a language-processing meta-analysis (Vigneau et al., 2011). With these coordinates, we extracted values representing the level of change in the neural signal in the corresponding brain space of our participants during Oldowan and Acheulian knapping tasks and rest periods. Data were included from 16 participants who learned to knap without verbal instructions (see Putt et al., 2017 for more information on the methods used to obtain and process neuroimaging data). The knapping values were statistically compared to the rest values using a Wilcoxon signed-rank test to determine if knapping significantly activated these visual and verbal WM areas.

Three visual WM regions were identified where the knapping signal is significantly higher than the rest signal, including the left frontal eye field and dorsolateral prefrontal cortex (dlPFC) in both hemispheres (see Fig. 2a). The frontal eye field forms part of a dorsal visual attention network (Corbetta and Schulman, 2002) and is only significantly activated during the Oldowan task. This result affirms what was found in the Oldowan-Acheulian contrast. The bilateral activation of dlPFC during the Acheulian task, however, is a novel result. The dlPFC is associated with a wide range of executive control functions, including planning, executing goal-directed behaviors, deductive reasoning, and decision-making (Coutlee and Huettel, 2012; Heekeren et al., 2006; Kaller et al., 2011). It is also one of the more important substrates for visual WM. The differential activation of bilateral dlPFC between the two toolmaking tasks suggests that making an Acheulian handaxe has a more ambiguous goal hierarchy and greater search depth than making Oldowan tools (Kaller et al., 2011), meaning that the sequence of actions needed to make an Acheulian handaxe is much less obvious. Also, Acheulian toolmaking requires mental generation of sequences and evaluation of the interdependency of individual actions, while Oldowan toolmaking is primarily based in visual search (see Fig. 1). These results further support three claims: 1) Acheulian toolmaking is a more cognitively demanding task than Oldowan toolmaking; 2) complex stone tool manufacture probably relies on a visual WM network; and 3) the appearance of the Acheulian industry in the archaeological record may mark a transition in the visual WM capabilities of early *Homo.*

(FIGURE 2 ABOUT HERE)

Of the seven verbal WM regions included in the analysis, there were only two areas significantly activated during the stone toolmaking tasks. These included the left dorsal pars triangularis, which forms the anterior portion of Broca’s area, and the right anterior middle frontal gyrus, which also overlaps with the anterior dorsal part of pars triangularis (see Fig. 2b). The signal in the left dorsal pars triangularis is significantly higher than the resting signal for both the Oldowan and Acheulian tasks, while only the Oldowan task signal is higher than the rest signal in the right anterior middle frontal gyrus. The increase in technical complexity with the advent of the Acheulian industry therefore cannot be attributed to the evolution of verbal WM per se.

Both of the noted areas are associated with phonological WM functions rather than semantic or sentence-level processing functions (Vigneau et al., 2011). For example, the former is activated in tasks that involve pseudo-word repetition (Warburton et al. 1996), word articulation versus word reading (McGuire et al. 1996), and reading consonant strings (Jessen et al., 1999). The function of the latter area is thought to be related to auditory selective attention without specificity for language (Petit et al., 2007). While these results could be attributed to including modern, language-using human subjects in the experiment or to the limited array of technologies tested (considered at length in the 2018 road map below), the most likely interpretation is that the activated areas are better characterized as general auditory WM centers that participate in tasks involving the monitoring of both auditory and verbal stimuli.

Macaques have neurons in this same cytoarchitectonic region of the ventrolateral PFC that respond to complex sounds, such as animal and human vocalizations, environmental sounds, and white noise (Romanski and Goldman-Rakic, 2002), indicating that the participation of this region in auditory WM functions long predates its use for language functions. Combined with the auditory-processing areas in the temporal lobe that come online during the Acheulian toolmaking task (Putt et al., 2017), the activated areas may participate in a perception-action cycle during stone tool production in which their discriminatory properties would be useful for distinguishing between meaningful sounds, including sounds that are informative about successful vs. unsuccessful flake removal, the size of the flake removed, and the presence of faults within the material.

To more explicitly inspect the amount of spatial overlap between visual and verbal WM, a third analysis was conducted that involved constructing 8 mm spheres around the coordinates of seven verbal WM cortical regions and eleven visual WM cortical regions from two unrelated meta-analyses (Vigneau et al., 2011; Wijeakumar et al., 2015) and plotting these spheres in the same brain space using Analysis of Functional NeuroImages (AFNI) software.

The results confirm that there is little overlap between verbal and visual WM centers in general; however, there are two regions where they converge (see Fig. 3a). This overlap occurs at the vPMC at the junction between pars opercularis and the precentral gyrus in both hemispheres, overlapping with Broca’s area in the left hemisphere. The left vPMC is also activated during Acheulian toolmaking in the Oldowan-Acheulian contrast conducted by Putt et al. (2017) and Stout et al. (2008; see Fig. 3b).

(FIGURE 3 ABOUT HERE)

The vPMC receives inputs from multiple sensory and association areas related to WM and is thought to maintain and monitor sensorimotor information in WM to make decisions about motor output (Pardo-Vazquez et al., 2011). It therefore could be an integration area where visual and auditory WM join to form higher-order categories of auditory-visual events, which would explain why this area is activated during WM tasks regardless of the mode of sensory information being processed. The vPMC is also the site of mirror neurons, which play an important role in relating perception to action (Grèzes et al., 2003).

DISCUSSION

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

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

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

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

TOWARDS A NEW ROAD MAP

While WM is implicit in the specifications of complex action recognition and imitation, as of yet, it is unclear what the role of WM is in Arbib's Mirror System Hypothesis. Until we have a fuller understanding of the different "types" of WM that exist and how they relate to one another evolutionarily, it will be difficult to specify its role in this hypothesis. Going forward, the 2018 road map should more explicitly consider the part that WM played in the evolution of language precursors, such as complex action recognition and imitation, pantomime, and protolanguage. Neuro-archaeological methodology should be further explored as a possible means to investigate the trajectory of verbal WM networks over the course of hominin evolution.

First we must test the hypothesis that verbal WM areas are recruited during stone toolmaking tasks because of the possibility that a lifetime of language use permanently alters modern human participants' functional neuroanatomy. Future studies could record the brain activity of non-human primates as they make chipped stone tools to test this assertion. Bonobos (*Pan paniscus*) and orangutans (*Pongo pygmaeus*) are capable of removing flakes from a core in a similar manner to Oldowan tool production (Wright, 1972; Toth et al., 1993), which would offer an appropriate comparison, as verbal WM areas are activated even during the Oldowan task. If homologous areas are inactive in non-human primates under similar conditions, then we could infer that the activation of these verbal WM areas reflects a human strategy of processing the same task by using language.

Second, we must test the hypothesis that the process of making later-occurring tools of greater complexity require more extended functions of verbal WM, such as semantic and sentence-level processing. To test this assertion, similar experiments should be conducted that look at the extent of verbal WM involvement during the production of increasingly more complex technologies that appear later in the archaeological record. For example, the cognitive abilities needed to haft stone points to wooden shafts with compound adhesives during the Middle Stone Age, including the capacity for multilevel operations, abstract thought, and recursion, have been directly compared to the sentence-level processing of language (Wadley, 2010).

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FIGURE CAPTIONS

Fig. 1. Goal hierarchy and production stages associated with Oldowan flaking (a-b) and early Acheulian handaxe manufacture (c-d). These particular goal hierarchies reflect the thought process of the first author while working toward the overarching goals of making the featured tools. Each goal can only be accomplished if all of its underlying subgoals are also accomplished. The Acheulian production stage (d) demonstrates how easy it is to snap a core if proper attention is not directed to each of the subgoals.

Fig. 2. Active visual WM (a) and verbal WM (b) areas during stone tool production tasks. Red circles represent WM coordinates determined by meta-analyses (Wijeakumar et al., 2015 in the case of visual WM and Vigneau et al., 2011 in the case of verbal WM). Only regions where the signal associated with the stone tool production tasks is significantly higher than the signal associated with rest periods are included. Significant Wilcoxin signed-rank tests where $p < 0.05$ are marked by an asterisk. Error bars in the bar plots represent 95% confidence intervals. Percentage signal change is in μM units.

Fig. 3. Ventral premotor cortex, where functional overlap occurs between visual WM and verbal WM in both hemispheres (a) and Acheulian tool manufacture in the left hemisphere (Putt et al., 2017) (b).

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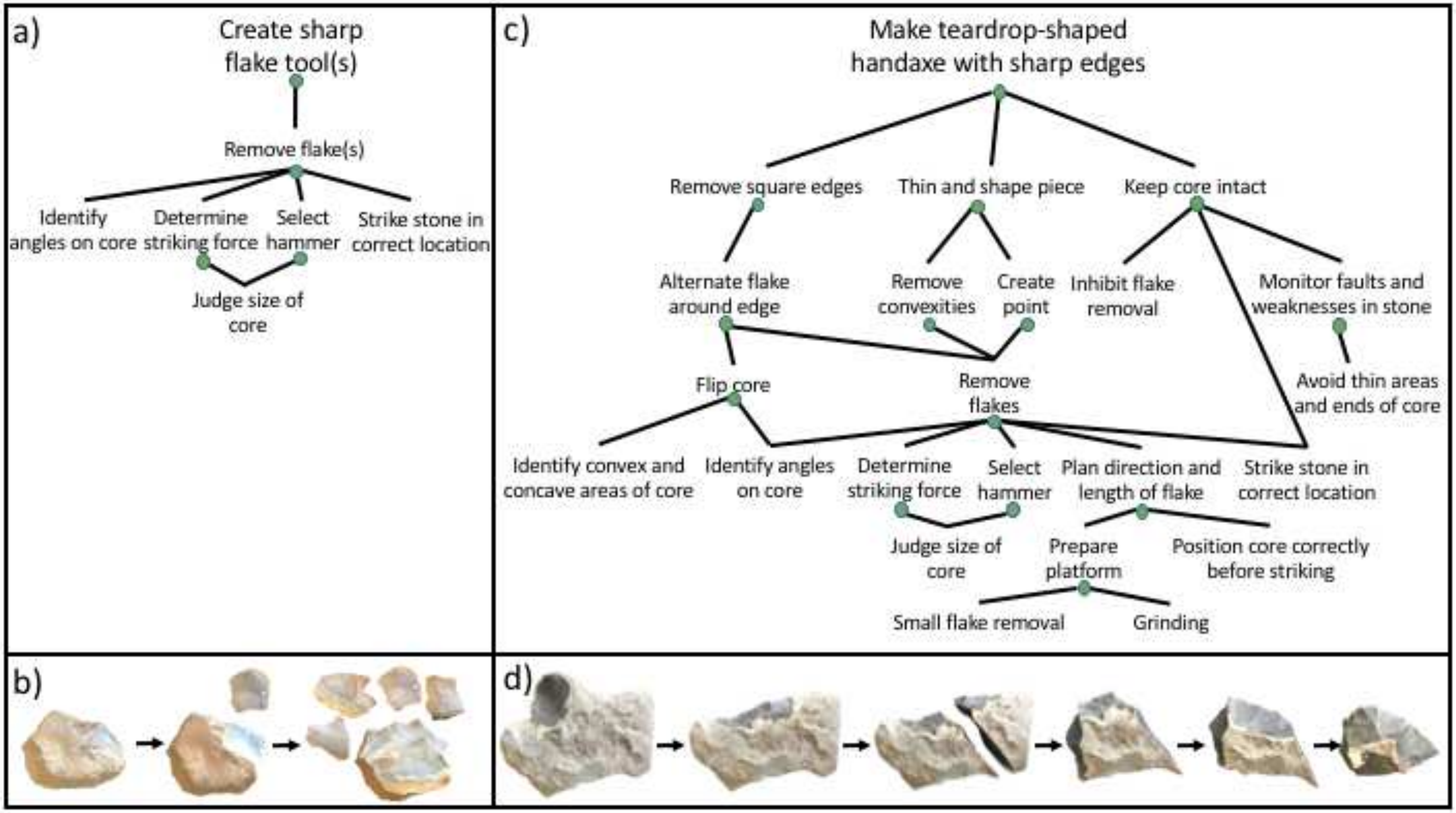

Figure

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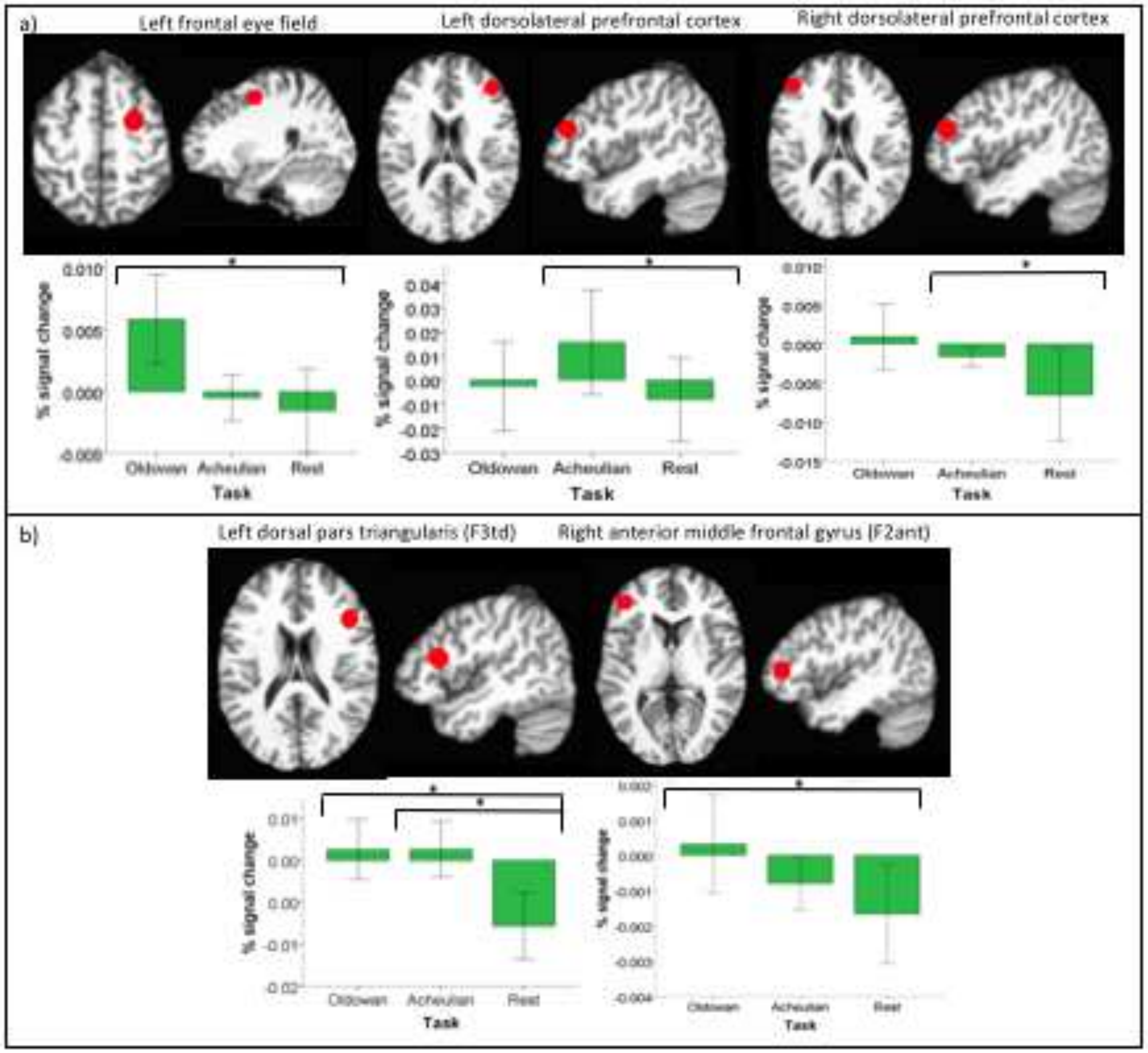

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